Plant functional traits associated with shoot flammability

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Fire is a common natural disturbance in many parts of the world, which changes species composition and ecosystem processes, shaping many of the world's biomes. Fire has been an important disturbance for hundreds of millions of years, since the origin of terrestrial plants. Several factors interact to determine fire behaviour, including the prevailing weather conditions, the topography of the landscape, and the fuels available for the fire to burn. The main fuels available to initiate and sustain wildfires are plants. Hence, to understand wildfire behaviour, it is essential to know how easily plants ignite and how well they burn; that is, we must be able to measure plant flammability.

Flammability is a complex plant trait that is not easy to measure and which differs across different plant parts or components. Flammability studies conducted on small plant components in the laboratory may not reflect how a plant will burn in nature. Furthermore, flammability research lacks a standard way of quantifying plant flammability in the laboratory. In this thesis, I seek to help address these shortcomings and gain a better understanding of plant flammability, first by comparing the flammability measurements at two different plant components (leaves and shoots) in the laboratory. Next, I investigated the influence of leaf morphological, chemical, and fuel architectural traits on flammability. Finally, I examined the role of species mixtures in causing variation in flammability, by burning fuel mixtures consisting of species of varying levels of flammability.

Comparing the flammability of fuels from different plant components (leaf- and shoot-level) (*Chapter 2*), I showed that flammability measurements between these fuels were uncorrelated and provided evidence that shoot flammability is likely to be better than leaf flammability at estimating the flammability of plants in the field, at least for canopy fuels. When investigating the relationship between leaf traits and shoot flammability using leaf-level morphological and chemical traits of 43 species collated from trait databases (*Chapter 2*), I demonstrated that leaf traits such as leaf dry matter content (LDMC), leaf thickness, leaf phenolics, and leaf lignin

were correlated with shoot flammability, and thus have potential as useful and easily-measured surrogates for flammability. To further investigate trait flammability relationships, I measured leaf and architectural traits of 65 indigenous and exotic New Zealand species, along with shoot flammability, on the same individuals of a species (*Chapter 3*). I provided further evidence that LDMC and leaf thickness were strongly correlated with shoot flammability, and that branching pattern (number of ramifications and sub-branches) was the most important architectural trait influencing shoot-level flammability. Other architectural traits, such as foliage and twig fraction mass and fuel bulk density, were also shown to be correlated to shoot flammability.

Given that fires often burn through vegetation that contains plant species of varying flammability, I investigated how the flammability of fuel mixtures was affected by the flammability of constituent species. Using shoot samples from two high flammability and two low flammability species (*Chapter 4*), I showed that the flammability of species mixtures was non-additive (i.e. disproportionately influenced by the flammability of the constituent species), and that the low flammability species significantly reduced flammability variables, such as burning time and total heat release of the species mixture.

I have demonstrated that shoot-level flammability measurements represent a more suitable laboratory-based means of quantifying canopy flammability than the more widely-used approach of measuring leaf-level flammability. Furthermore, I have quantified the effects of leaf and architectural traits on shoot flammability and identified key traits, such as LDMC, which can be used as surrogates for plant flammability. Finally, I have identified the role of plant species of varying flammability in changing the fire behaviour of species mixtures, demonstrating the mechanisms by which low flammability plants can be used to reduce fire impacts. These findings not only contribute to a greater understanding of how plants burn, they should prove useful for model-based approaches to predicting changes to fire regimes, and provide crucial information to fire managers seeking to mitigate fire damage in an increasingly fire-prone world.

Keywords: branching pattern, calorimeter, crown fire, fire behaviour, fire management, fuel mixture, functional traits, green firebreaks, leaf chemicals, leaf flammability, low flammability, non-additivity, plant architecture, plant flammability, shoot flammability, wildfire

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List of abbreviations

a.s.l	Above sea level
ADC	Acid detergent cellulose
ADL	Acid detergent lignin
AIC	Akaike information criteria
AICc	Corrected akaike information criteria
ANOVA	Analysis of variance
AT	Angiosperm tree
BD	Bulk density
BPRP	Branching pattern on ramification point
BPSO	Branching pattern on stream order
CT	Conifer tree
FB	Forb
FBD	Fuel bulk density
FFM	Foliage fraction mass
FMC	Fuel moisture content
FN	Fern
GLM	Generalized linear model
GR	Grass
HOC	Heat of combustion
HRR	Heat release rate
LA	Leaf area
LDM	Leaf dry mass
LDMC	Leaf dry matter content
LFMC	Live fuel moisture content
LMC	Leaf moisture content
LN	Liana
LPG	Liquid petroleum gas
LT	Leaf thickness
MAE	Mean absolute error
MC	Moisture content

N	Nitrogen
ODC	Oxygen depletion calorimetry
P	Phosphorus
PCA	Principal component analysis
PHRR	Peak heat release rate
r	Correlation co-efficient
R^2	Regression co-efficient
RMF	Residual mass fraction
RMSE	Residual mean square error
SA:V	Surface area to volume ratio
SE	Standard error
SLA	Specific leaf area
SS	Shrub
SV	Shoot volume
TBT	Total burn time
TDMC	Twig dry matter content
TFM	Twig fraction mass
THR	Total heat release
TPHRR	Time to peak heat release rate
TTI	Time to ignition
UDL	Universal data logger
VIF	Variance inflation factor
VOC	Volatile organic compounds

Chapter 1
Introduction

1.1 The importance of studying wildfire

Fire is a widespread ecological process and a common phenomenon in many ecosystems worldwide (Bowman *et al.* 2009). It is a natural disturbance agent that has profound impacts in shaping ecosystem composition, structure, and processes, as well influencing biome distribution (Ahlgren & Ahlgren 1960; Bond & Keeley 2005; Jin & Roy 2005; Chen 2006). These processes have occurred for hundreds of millions of years (Bond & Keeley 2005; Belcher *et al.* 2013) and acted as a major ecological and evolutionary driver to modify Earth's biodiversity (Pausas *et al.* 2017; He *et al.* 2019). Moreover, fires can assist in controlling pathogens and also contribute to carbon and nutrient cycling within ecosystems (Flannigan *et al.* 2009a; O'Donnell *et al.* 2009). However, as well as being a key disturbance in many ecosystems, fire also poses severe threats to wildlife, human lives, infrastructure, and farmland in the wildland-urban interface (Bowman *et al.* 2009). Projected estimates of climate change by the International Panel on Climate Change (IPCC) point to rising temperatures, stronger winds, and more frequent droughts and other extreme climatic events in many parts of the world (IPCC 2015). Hence, fires are expected to become more intense and frequent (Flannigan *et al.* 2000; Flannigan *et al.* 2006; Krawchuk *et al.* 2009; Williams *et al.* 2013).

Although the global annual area burned has actually declined in last two decades (Giglio *et al.* 2013; Doerr & Santín 2016; Andela *et al.* 2017), the frequency of large, uncontrolled, high-intensity mega-fires has increased worldwide, posing greater threats to biodiversity, human health and property, and the economy (San-Miguel-Ayanz *et al.* 2013; de la Barrera *et al.* 2018). Recent incidences of catastrophic fires in the United States of America, Chile, Canada, Australia and Mediterranean Europe (Anonymous 2017; de la Barrera *et al.* 2018; Gómez-González *et al.* 2018) provide examples of the extreme wildfires that forest managers, landowners, and farmers may face in the future. While fire is vital to many ecosystems for its ecological and evolutionary roles in maintaining biodiversity, uncontrolled wildfire can be devastating for human lives, properties, and societies. Therefore, understanding the mechanisms underpinning fire behaviour will help us to manage vegetation to both conserve biodiversity and reduce the negative impacts of uncontrolled wildfires.

1.2 Wildfire, fuels, and flammability

Wildfire behaviour is determined by several interacting factors, including the prevailing weather conditions, the topography of the landscape, and the fuels available for the fire to burn. Fuel abundance, composition, structure, and arrangement will result in considerable changes in wildfire behaviour across a landscape (Papió & Trabaud 1990; Schoennagel *et al.* 2004). Depending on the fuels involved during the fire, wildfire is classified into three categories: ground fire, surface fire, and crown fire (Brown & Davis 1973). These fires vary in their intensity, behaviour, and impact on ecosystems. Ground fires burn underground fuels, typically buried organic matter, including peat, coal, and tree roots (Cochrane 2010). Ground fires are generally low-intensity fires that can grow into medium-intensity surface fires that mainly burn on the surface of the ground and hardly pass above tall shrub level (Oosting 1944; Cochrane 2010). They mostly consume litter, such as dried leaves, twigs, needles, and herbaceous vegetation, shrubs, and saplings under the crown. With favourable conditions, surface fires can develop into crown fires through ladder fuels connecting surface fuels to crown fuels. Crown fires are a complex and high-intensity fires that usually occur under extreme fire weather conditions (Wagner 1977; Alvarez *et al.* 2013). Crown fires can be initiated directly in a tree crown through lightning-based ignitions, but most destructive crown fires start from surface fires, where understorey shrubs and trees assist in transitioning fire from the surface to the crown (Mitsopoulos & Dimitrakopoulos 2007). Hot and dry weather with high winds will increase the rate of spread and fire intensity in the canopy, resulting in erratic and dangerous fire behaviour (Wagner 1977). While only specific fuels are involved in ground or surface fires, crown fire includes and affects all the fuel complexes from the ground to treetop. Given that wildfire behaviour is closely linked with fuel characteristics, understanding the burning properties or flammability of the fuel is vital to study wildfire behaviour.

Flammability is a multivariate trait, which generally describes the ease of ignition and maintenance of combustion of a fuel (White & Zipperer 2010). Flammability is an inherent characteristic of plants that indicates a plant's ability to burn when exposed to an ignition source (Gill & Zylstra 2005). Flammability is complex to measure and there is no direct measurement. It is expressed and quantified through different response parameters which vary considerably depending on where the measurements are conducted (i.e. field or laboratory) and associated fuels and methodologies. In general, flammability is considered to have four variables: ignitability (ease of ignition), combustibility (intensity at which a plant burns), sustainability (length of time a plant continues to burn) and consumability (how much of a plant is burnt)

(Anderson 1970; Martin *et al.* 1994). Other researchers have characterized flammability in different ways and divided it into several axes or dimensions, such as ignitibility that describes the probability of ignition, flame spread rate that determines the area burned, and rate of heat release and/or amount of heat released that describe smouldering combustion (Schwilk 2015; Pausas *et al.* 2017; Prior *et al.* 2018). Despite these different approaches to measure flammability, I have used the approach proposed by Anderson (1970) and Martin *et al*. (1994), which consists of four components of flammability expressed by various parameters (White & Zipperer 2010). Flammability varies widely among species (Calitz *et al.* 2015; Simpson *et al.* 2016; Wyse *et al.* 2016) and species with high flammability are likely to enhance the intensity and rate of spread of fire, whereas low flammability species may hinder fire spread (Brooks *et al.* 2004; Beckage *et al.* 2009; Mola *et al.* 2014; Padullés Cubino *et al.* 2018). Therefore, the quantification of plant flammability is vital to understand the behaviour of fire (Gill & Zylstra 2005; White & Zipperer 2010). However, measuring the flammability of a plant is a difficult task due to the variation of flammability in different components of the plant (e.g. leaf, shoot and whole plant) and the complex interaction of flammability with factors such as plant size and age, moisture content and plant architecture (White & Zipperer 2010). Thus, scientists need to be careful when deciding how best to measure the flammability of a plant.

1.3 Flammability experiments conducted on different plants components

Plant flammability has been measured in various ways by different authors, on different plant components, often with little standardisation (White & Zipperer 2010). Mostly, small plant components, such as leaves, small twigs, litter, or woody debris are used to measure flammability in the laboratory (Behm *et al.* 2004; Scarff & Westoby 2006; Curt *et al.* 2011; Murray *et al.* 2013; Cornwell *et al.* 2015; Mason *et al.* 2016; Pausas *et al.* 2016; Zhao *et al.* 2018). Although such flammability tests can provide useful insights for fire risk assessment, there is uncertainty around the relevance of these small-scale experiments for our understanding of broader-scale issues, such as fire behaviour and the prediction of whole plant flammability (Fernandes & Cruz 2012; Bowman *et al.* 2014; Schwilk 2015). The main difficulty for predicting fire behaviour in field conditions is that consideration of the whole plant architecture, surrounding vegetation, and the climatic condition is vital (Jaureguiberry *et al.* 2011; Pérez-Harguindeguy *et al.* 2013; Schwilk 2015). Also, the physical, physiological, and chemical traits of plants will contribute to flammability (Papió & Trabaud 1991; Schwilk 2003), influencing vegetation-fire relationships.

The most comprehensive way to measure flammability is to burn the entire plant, but this is an expensive and complex task (Gill & Moore 1996). The burning of the whole plant is problematic and, in many cases, does not allow for many samples to be tested in a given time frame, making it a hard-to-measure trait (White & Zipperer 2010; Jaureguiberry *et al.* 2011). Hence, most researchers utilize small plant components to measure flammability under the assumption that this represents whole-plant flammability. Also, due to the variability in flammability attributes, different plant components (leaf, litter, twig, bark, and branch) have been utilised in preference to others by different authors. Considered more flammable than other components, leaves are frequently used in flammability experiments. Both fresh and dead leaves (the latter as litter) are the very first fuel that burns during canopy and surface fires, respectively (Midgley *et al.* 2011; Murray *et al.* 2013). Because experiments on litter fuels can be managed easily, considerable research on flammability has been carried out using leaf litter (Scarff & Westoby 2006; Plucinski & Anderson 2008; Curt *et al.* 2011; Ganteaume *et al.* 2014; Kauf *et al.* 2015). Also, several studies (Gill & Moore 1996; Ganteaume *et al.* 2013a; Murray *et al.* 2013, Grootemaat *et al.* 2015, Krix *et al.* 2019) have measured fresh leaf flammability, due to its tractable size and the ability to burn many samples in devices such as a cone calorimeter, epiradiator or muffle furnace. However, very few studies have measured bark flammability (Frejaville *et al.* 2013; Dehane *et al.* 2015; Grootemaat *et al.* 2017b), twig flammability (Weise *et al.* 2005; Belcher *et al.* 2010), and shoot flammability (Jaureguiberry *et al.* 2011; Burger & Bond 2015; Calitz *et al.* 2015; Wyse *et al.* 2016; Battersby *et al.* 2017; Padullés Cubino *et al.* 2018).

Measurement of the flammability of these different plant components has often been undertaken to provide information that might help suppress fires and to reduce damage to ecosystems and society. However, this applied goal has proved difficult, as we lack a standard way of measuring flammability that best represents the flammability of the whole plant. As plant flammability research has developed over time, scientists have struggled to determine the best method and fuel-level at which to measure flammability (White & Zipperer 2010). Among the plant components used for measuring flammability, which one will best represent the flammability of the whole plant? Burning a whole plant is problematic and expensive, whereas burning a leaf or twig cannot represent the architecture of the plant. However, burning a shoot of a plant (Jaureguiberry *et al.* 2011) and measuring the flammability (Fig. 1.1) may better represent the whole plant as it consists of the leaves, twigs, and branching pattern and hence preserves the architecture of the plant. Shoot-level flammability is recommended as a standard approach to measuring flammability in the trait measurement handbook (Pérez-Harguindeguy *et al.* 2013),

that is reliable and can provide consistent flammability data across species from different functional groups (Calitz *et al.* 2015; Wyse *et al.* 2016). Shoot-level flammability measurements appear to be an easy and inexpensive method of acquiring flammability data from a large number of samples from different species. Hence, shoot flammability measurements open a new horizon of fire ecology research into trait-flammability relationships, providing a better understanding of the mechanisms that determine how well different species burn.

Figure 1.1 Method of taking flammability measurements using plant shoots: a) Placing and preheating of sample; b) Sample ignition with blowtorch; c) Measurement of flammability variables. (species: *Kunzea robusta*).

1.4 Plant functional traits and flammability

Plant functional traits are those morphological, physiological, and phenological characteristics that determine the response of plants to particular environmental conditions (Pérez-Harguindeguy *et al.* 2013). Traits are also important to describe ecosystems function and to quantify plant performance and survival in a given environment (Violle *et al.* 2007). The study of functional traits facilitates an understanding of how plant species contribute to different ecosystem processes and functions (Violle *et al.* 2007; Soudzilovskaia *et al.* 2013; Yang *et al.* 2015; Kimball *et al.* 2016), as well as how they respond to different ecosystem disturbances (Suding *et al.* 2008). In the field of ecology, plant functional traits are increasingly used to identify links between species' characteristics, distribution, and community assembly (Poff 1997). Growing research on plant functional traits worldwide attempts to understand how patterns of plant functional variation correlate with ecosystem changes. Evidence of global patterns in functional trait variation, such as the leaf economics spectrum (Wright *et al.* 2004; Osnas *et al.* 2013) and the wood economics spectrum (Chave *et al.* 2009), suggests that trait-based ecology is a useful approach for predicting how ecosystems might be altered with changing environments (Lavorel & Garnier 2002).

There are many plant traits (morphological, anatomical, biochemical, physiological or phenological) that are measured worldwide to explore the interaction between local vegetation and the associated biotic and abiotic environment (McGill *et al.* 2006). The trait-based approach is popular and is used in several branches of ecology, e.g. plant ecology, functional ecology, community ecology, plant migration and invasion ecology, disturbance ecology and plant geography (Grime 1974, 1977; Schurr *et al.* 2005; Kraft *et al.* 2008; Paula & Pausas 2008; Swenson & Weiser 2010). Around 750 plant traits (reproductive and vegetative) are recorded in global plant trait archives (Kattge *et al.* 2011) and measured as continuous and categorical variables. In addition, traits are often categorised into "soft" and "hard" traits, based on the ease of the methods used to measure them (Hodgson *et al.* 1999). Soft traits are easy to measure, less difficult and expensive to quantify, and include traits such as specific leaf area, plant height, and leaf dry mass (Cornelissen *et al.* 2003). Hard traits are often complex to measure as they may require manipulative experiments, expensive equipment, or multiple measurements over time; however, they are closely linked to plant function, and include traits such as photosynthetic rate, respiration, transpiration or growth rates, and stomatal conductance (Hodgson *et al.* 1999; Cornelissen *et al.* 2003). The flammability of plants is influenced by a combination of plant functional traits (Jaureguiberry *et al.* 2011), and all the flammability variables are greatly affected by multiple traits on different plant components (leaves, branches, stems). Under similar environmental conditions, some plants burn better than others, and this mostly depends on the plants' intrinsic morphological and chemical traits (Gill & Moore 1996; Murray *et al.* 2013).

1.4.1 Leaf-level traits

Leaf-level traits are strongly related to plant flammability variables. Leaves are considered to be the most important flammable plant components (Gill *et al.* 1996; Etlinger & Beall 2005) because the leaves are the fine fuel most likely to ignite during a fire (Pickett *et al.* 2009; Murray *et al.* 2013). Both surface fires (litter) and canopy fires (fuel held on the plant, including green leaves) depend on leaf characteristics. Leaf dimensions (size, thickness, and shape) are important parameters related to plant flammability. Plants with larger leaves produce a litter bed structure with better ventilation and available oxygen and faster flame spread rate that burns rapidly, whereas small leaves tend to produce tightly packed litter bed that burns slowly (Scarff & Westoby 2006; de Magalhaes & Schwilk 2012; Van Altena *et al.* 2012). Conversely, plants with small leaves often have high flammability of live parts (shoots and branches) that are retained on the plant, as they dry faster and make the plants more flammable (Schwilk 2015).

Therefore, the same plant species that retard surface fire due to low-flammability leaf litter may increase canopy fire through highly flammable canopy structures (Scarff & Westoby 2006).

Leaf moisture content is another critical characteristic related to flammability (Bilbao *et al.* 1996; Etlinger & Beall 2005; Zhao *et al.* 2014). Species with high leaf moisture content are low in flammability because of the high heat required to ignite or burn such fuels (Hawley 1926; Fons 1946; Verbesselt *et al.* 2002). This is a highly important trait that correlates strongly with fire ignition or spread rate (Dimitrakopoulos & Papaioannou 2001; Sun *et al.* 2006; Alessio *et al.* 2008; Plucinski & Anderson 2008) and affects both crown and surface fires. It also assists in decreasing the combustibility and fire spread rate (Pyne *et al.* 1996). Moreover, both the surface area to volume ratio and specific leaf area is high in plants with larger and thinner leaves; this enhances ignitibility and combustibility (Montgomery & Cheo 1971; Gill & Moore 1996; Simpson *et al.* 2016), because moisture is lost more easily through heating and drying on a larger area (Brown 1970; Saura-Mas *et al.* 2010). Recently, specific leaf area has been considered a good determinant of ignitibility because it includes the density of the material rather than only the surface area and volume dimensions ($\mathrm{SLA} = 1/thickness \times 1/density$) (Murray *et al.* 2013; Grootemaat *et al.* 2015). Thick leaves tend to decrease flammability as fleshy tissue takes longer to ignite (Murray *et al.* 2013; Bowman *et al.* 2014). In addition, leaf nutrients and volatile organic compounds, as well as the presence of flammable oils and minerals, influence plant flammability (White & Zipperer 2010; Pausas *et al.* 2016). These are naturally-occurring plant chemicals present in a diverse array of species. Among volatile organic compounds, phenols and terpenes are highly related to the flammability of plants (White 1994; Cornelissen *et al.* 2003), and the presence of these molecules lessens the ignition time and increases flammability (Owens *et al.* 1998; Alessio *et al.* 2008; Ormeno *et al.* 2009; Pausas *et al.* 2016). Similarly, leaf nitrogen is considered to increase the flammability of plants by increasing heat release (Mason *et al.* 2016), whereas leaf phosphorus acts as a fire retardant and decreases flammability by reducing heat release (Scarff & Westoby 2008; Scarff *et al.* 2012).

1.4.2 Shoot-level traits

Shoots can retain the architecture of plants; hence, shoot-level traits are expected to influence flammability. Bulk density and fuel load are the properties of a shoot that are considered critical determinants of flammability (Hoffmann *et al.* 2012; Marino *et al.* 2012). Fuel bulk density (mass of fuel per volume of the fuel) affects flammability because it is highly correlated with

radiant heat transfer. Increases in bulk density result in more heat being released by the fire, and a higher fire spread rate (Rothermel 1972). Closely positioned leaves and branches in a plant transfer radiant heat quickly from one leaf or branch to another and increase flammability (Schwilk 2015), although very densely packed fuels may become oxygen-limited, which can extinguish the fire (Schwilk 2015). Similarly, a high fuel load is also related to increasing heat release and burn times, enhancing flammability (Saura-Mas *et al.* 2010).

The amount of dead material is another indicator of plant flammability: dead plant material is very low in moisture content (Page *et al.* 2012) and is easily burnt, which makes it more flammable than the living parts (Dent *et al.* 2019). Some species retain dead branches, leaves, twigs, and bark that help to spread fire into the canopy (Schwilk 2003; Keeley 2012), whereas other species shed their dead branches to reduce the likelihood of canopy fire (He *et al.* 2012). Also, fuels with high foliage density or foliage fraction mass, burn readily due to available fine fuels and fuel connectivity (Etlinger & Beall 2005). Similarly, branching pattern or ramification and vertical arrangement of fuels improves fuel connectivity and increases flammability by facilitating the easy spread of heat and flames.

1.5 Research objectives and thesis outline

In this thesis, I aim for a better understanding of plant flammability by identifying the suites of functional traits that can determine shoot flammability. To fulfil this aim, I have investigated the following questions in *Chapters 2-4*:

Q1) How do flammability measurements vary between leaf and shoot levels and which of these is a better way to measure plant flammability? (*Chapter 2*)

Q2) Which leaf-level morphological and chemical traits most affect shoot flammability? (*Chapter 2*)

Q3) How do leaf functional traits and fuel architectural traits affect shoot flammability? (*Chapter 3*)

Q4) Can we predict shoot flammability from functional traits? (*Chapter 3*)

Q5) How does flammability vary in shoot-level mixed-fuel combustion? (*Chapter 4*)

Q6) What are the roles of the constituent species in mixed-fuel combustion? (*Chapter 4*)

The whole thesis consists of a general introduction to outline the background of this study (*Chapter 1*), three data chapters dealing with the questions described above (*Chapters 2-4*), and a general discussion (*Chapter 5*) to synthesise the findings from these questions. These three data chapters are written as manuscripts for submission to international journals. *Chapter 2* has already been accepted for publication in the *Journal of Ecology* while *Chapters 3 & 4* will be submitted soon. Because of this format, there is some duplication between the different data chapters, the general introduction, and the discussion chapter. However, each of these chapters deals with different questions, requiring varied methodological approaches as briefly summarised below.

Chapter 2 investigates *Q1* and *Q2* of the thesis. The level of fuel (i.e. the plant used, e.g. leaf or shoot) is an issue in understanding fire behaviour because researchers use different levels of fuels, mostly small plant components such as leaves or twigs, to characterise plant flammability. However, these laboratory experiments using small plant components have been criticised for not representing the flammability of the whole plant (Fernandes & Cruz 2012). To address *Q1*, I compared the flammability at two different fuel levels: leaf-level (most commonly used in flammability studies) and shoot-level (which retains aspects of plant architecture) to identify the most appropriate way of quantifying plant flammability. Here, I used existing species-level mean flammability data of 43 species at both leaf and shoot levels. To identify which fuel-level better represents the flammability of the plant, I then compared the flammability measured at these two fuel levels with the flammability of the plants in the field as observed by fire managers throughout New Zealand (Fogarty 2001).

Plant functional traits are likely to influence the flammability. Leaves are the first component to ignite during a fire; therefore, leaf morphology and chemicals are expected to affect flammability. To address *Q2*, I examined relationships between shoot flammability and leaf morphological and chemical traits, using existing data of shoot flammability measurements and data on leaf morphological and chemical traits of the same species collated from national trait databases.

Chapter 3 examines *Q3* and *Q4* and further explores trait flammability relationships at the shoot-level, including fuel architectural traits. In *Chapter 2*, the trait-flammability relationships

were examined using species mean data on functional traits and flammability compiled from published literature, where both the functional traits and flammability variables were measured on different individuals of each species. In contrast, *Chapter 3* involved the measurement of functional traits and flammability on the same individual plants for 65 species. This allowed examination of whether the trait-flammability relationships determined using species-level means from trait databases held when they were measured on the same plants. Furthermore, considering the importance of plant architecture in affecting fire spread and intensity, I measured shoot-level architectural traits to examine the influence of fuel architecture in influencing the flammability of plants at shoot-level. Finally, I investigated how well shoot flammability could be predicted, based on modelling using both the leaf and architectural traits.

The flammability of a species is essential to understand specific fuel hazards and the fire behaviour of vegetation comprised of monospecific fuel. However, in nature, different species co-occur together and fire burns through the fuels of adjacent species. While *Chapters 2 and 3* provide knowledge on the flammability of many species burnt separately, *Chapter 4* investigates the flammability of mixed-species fuels to better reflect the natural vegetation where fuels from different species are burnt at the same time. Here, I investigated *Q5* and *Q6* by burning different combinations of shoot samples from four different species of varying flammability in a specialised calorimeter, using oxygen depletion calorimetry. In this experiment, I measured several flammability variables (e.g. heat release rate, total heat release) that are closely related to the fire behaviour of vegetation at the field to get better insights on the variation of fire behaviour in mixed-fuel combustion. This will examine whether the flammability of species mixtures differs to that of the constituent species, and how the flammability of the constituent species each affect the flammability measurements of the mixture.

Finally, *Chapter 5* synthesises the findings from these preceding chapters and discusses them in the context of the broader literature. The implications of these findings in terms of fire and vegetation management are discussed, along with the direction for future research to fill some of the remaining knowledge gaps.

Chapter 2

Shoot flammability is decoupled from leaf flammability, but controlled by leaf functional traits

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This study was conceived by TC, AA, GP, and SW and designed by AA, TC, GP, SW, and HB. Analyses were conducted by AA, HB, SW, JS, and GP. AA wrote the first draft, which was then revised and approved by all co-authors.

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2.1 Abstract

1. Flammability is an important plant trait, relevant to plant function, wildfire behaviour, and plant evolution. However, systematic comparison of plant flammability across ecosystems has proved difficult because of varying methodologies and assessment of different fuels comprising different plant components. We compared the flammability of plant species at the leaf-level (most commonly used in flammability studies) and shoot-level (which retains aspects of plant architecture). Furthermore, we examined relationships between leaf functional traits and flammability to identify key leaf traits determining shoot-level flammability.

2. We collated and analysed existing leaf- and shoot-level flammability data from 43 common indigenous perennial New Zealand plant species, along with existing data on leaf morphological and chemical traits.

3. Shoot-level flammability was decoupled from leaf-level flammability. Moreover, leaf-level rankings of flammability were not correlated with rankings of flammability of plants derived from expert opinion based on field observations, while shoot-level rankings had a significant positive relationship. Shoot-level flammability was positively correlated with leaf dry matter content (LDMC), phenolics and lignin, and negatively correlated with leaf thickness.

4. Our study suggests that shoot-level measurements of flammability are a useful and easily replicable way of characterising the flammability of plants, particularly canopy flammability. With many parts of the world becoming more fire-prone, due to anthropogenic activities, such as land-use change and global warming, this finding will help forest and fire managers to make informed decisions about fuel management, and improve modelling of fire-vegetation-climate feedbacks under global climate change. Additionally, we identified some key, widely measured leaf traits, such as LDMC, that may be useful surrogates for plant flammability in global dynamic vegetation models.

2.2 Introduction

Plant flammability describes the ability of plant biomass to ignite and sustain a flame when exposed to fire (Gill & Zylstra 2005; Pausas *et al.* 2017). Plants fuel most of the wildfires on earth and plant flammability plays a central role in determining the intensity and severity of wildfires (Beckage *et al.* 2009; Simpson *et al.* 2016; Pausas *et al.* 2017). In recent years, wildfire activity has increased in terms of size and the frequency of high severity fires, and many parts of the Earth that are not normally fire-prone have experienced devastating wildfires (Miller *et al.* 2009; Flannigan *et al.* 2013; Doerr & Santín 2016; Westerling 2016; Anonymous 2017). This trend is mainly due to anthropogenic activities (such as land-use change and extensive fire prevention activities), and human-induced climate change, which contributes to higher temperatures, increased drought frequency and intensity, altered forest composition and productivity, increased vegetation dryness, and longer fire seasons (Flannigan *et al.* 2009b; Jolly *et al.* 2015; Abatzoglou & Williams 2016; Le Page *et al.* 2017). Management of wildfires requires accurate characterisation of plant flammability (Dimitrakopoulos 2001; Chuvieco *et al.* 2009; White & Zipperer 2010). An understanding of plant flammability can also inform fundamental research. For instance, flammability is recognised as a core plant functional trait (Cornelissen *et al.* 2003; Perez-Harguindeguy *et al.* 2013) and is a key factor in understanding the evolution of land plants (Schwilk & Ackerly 2001; Pausas & Moreira 2012), particularly given the 420 million-year shared history of plants and fire (Glasspool *et al.* 2004; He *et al.* 2016; Scott 2018).

Flammability can influence the fitness, survival, reproduction, and distribution of plants, as seen by the evolution of flammability strategies in fire-prone environments (Mutch 1970; Bond & Midgley 1995; Pausas *et al.* 2017). Recently, there have been renewed efforts in plant flammability research to tackle fundamental topics such as the evolution of plant flammability (Battersby *et al.* 2017; Pausas *et al.* 2017; Archibald *et al.* 2018), and in an applied context to provide information useful for fire management (Wyse *et al.* 2016; Krix & Murray 2018; Zylstra 2018), building on past work in such areas (Mutch 1970; Gill 1981; Bond & Midgley 1995; Kerr *et al.* 1999). However, there is still considerable debate on how best to measure plant flammability and therefore, how to appropriately quantify this important plant trait (Schwilk 2015; Varner *et al.* 2015).

Quantification of flammability is not straightforward. Plant flammability can be separated into four different variables: (1) ignitibility (ignition delay time or temperature required to ignite any fuel); (2) combustibility (how much temperature the fuel emits or heat release rate); (3) sustainability (how long the fuel continues to burn); and (4) consumability (how much of the fuel is consumed during a fire) (Anderson 1970; Martin *et al.* 1994; White & Zipperer 2010). Moreover, plant flammability has been measured using a variety of methods (White & Zipperer 2010), at multiple levels (leaf, shoot, whole plant) and for different fuel types (canopy and litter) (Jaureguiberry *et al.* 2011; Schwilk & Caprio 2011; Pausas & Moreira 2012; Murray *et al.* 2013; Pausas *et al.* 2016). Most flammability experiments have been conducted in the laboratory on small plant components (i.e. leaves, leaf litter, small twigs or needles, bark, woody debris) due to ease of sample collection and manipulation during burning (Ganteaume *et al.* 2013a; Kauf *et al.* 2015; Mason *et al.* 2016; Grootemaat *et al.* 2017b; Zhao *et al.* 2018). It has been argued that these fine-level laboratory tests do not scale up to predict canopy flammability or crown fire in the field, at least in part because they do not adequately account for plant architecture (Fernandes & Cruz 2012).

High-intensity crown fires are mostly initiated from surface fuels that, with the necessary environmental conditions, climb into the canopy using understorey shrubs and low-lying branches as ladder fuels (Wang *et al.* 2016; Blauw *et al.* 2017). Some ecosystems (e.g. grasslands, shrublands, and North American boreal forest) are more prone to crown fires due to their vegetation structure, where canopies extend to the ground and act as ladder fuels (Bradstock & Gill 1993; Kafka *et al.* 2001). With the increasing occurrence of crown fires worldwide, there is an urgent need to better characterise canopy fuel characteristics (Cruz *et al.* 2003; Mitsopoulos & Dimitrakopoulos 2007). While burning entire plants is more appropriate for understanding crown fire behaviour (Stephens *et al.* 1993; White *et al.* 1997; Etlinger & Beall 2005), this approach is logistically challenging and expensive (Jaureguiberry *et al.* 2011; Pausas & Moreira 2012). In response to this challenge, a low-cost device for measuring shoot-flammability was developed by Jaureguiberry *et al.* (2011) and has been promoted because it facilitates rapid measurement of the relative flammability of many species (Perez-Harguindeguy *et al.* 2013; Schwilk 2015). Additionally, the plant flammability rankings derived from these shoot-level measurements are highly correlated with independent rankings determined by expert opinion based on observation of plant flammability in the field (Wyse *et al.* 2016), suggesting that the shoot-level measurements might scale up to canopy flammability. Despite these advances, the outcomes from different methodologies and levels of flammability measurements are often incomparable, providing conflicting information when attempts are

made to upscale to whole plant flammability or fire behaviour in the field (White & Zipperer 2010). Thus, to better characterise plant flammability and to improve predictions of flammability across different fuel levels, it is essential to compare the flammability of different fuel types quantified using different methodologies.

The flammability of plants is likely to be related to their functional traits. Some traits, such as the retention of dead plant matter, presence of volatile chemicals, and high leaf dry matter content, can enhance flammability, whereas other traits, such as high moisture content, thick leaves, and high fuel density, decrease flammability (Anderson 1970; Cornelissen *et al.* 2003; Murray *et al.* 2013; Pausas *et al.* 2016; Simpson *et al.* 2016). Among these traits, leaf physical and chemical traits affect ignitibility, combustibility and sustainability of single leaves (Alessio *et al.* 2008; Murray *et al.* 2013; Grootemaat *et al.* 2015), whereas fuel loading, branching pattern and other architectural traits are important determinants of whole-plant flammability (Schwilk 2003; Fernandes & Cruz 2012; Zylstra *et al.* 2016). Several studies have sought to predict flammability and fire behaviour from functional traits at leaf, litter, whole plant, and ecosystem levels (Schwilk & Caprio 2011; Grootemaat 2015; Simpson *et al.* 2016; Zylstra *et al.* 2016). It is expected that shoot-level measurements provide an appropriate quantification of canopy flammability (Schwilk 2015) as the shoots preserve the architecture of the plant (Jaureguiberry *et al.* 2011; Wyse *et al.* 2016). Because of this, understanding the relationships between traits and shoot flammability should enhance our knowledge of how certain species may influence crown fires.

While several studies have estimated plant and community flammability at individual-, ecosystem-, or biome-level by measuring shoot-level flammability (e.g. Jaureguiberry *et al.* 2011; Burger & Bond 2015; Calitz *et al.* 2015; Wyse *et al.* 2016; Padullés Cubino *et al.* 2018), few have quantitatively assessed trait-flammability relationships. Calitz *et al.* (2015) compared ordinal trait values, including leaf size, leaf texture, leaf density and twigginess (number of twigs per unit volume), to shoot flammability, and found that plants with small leaves and high twigginess had relatively high flammability. However, Calitz *et al.* (2015) identified few robust trait-flammability relationships and concluded that other, unmeasured traits better predicted flammability, or that the measured traits interacted to influence flammability. Leaves are usually the first components of a plant to be ignited and mostly burn along with terminal branches during fires (Midgley *et al.* 2011; Murray *et al.* 2013; Belcher 2016), and so leaf traits are expected to influence plant flammability. In addition, leaves are a fuel component that is

strongly linked to fire behaviour, and leaf traits are increasingly used to understand the pattern of fire behaviour in the field (Schwilk & Caprio 2011; Zylstra *et al.* 2016).

Leaf traits can also reflect the architecture of a shoot as a narrow, frequently-branched shoot often has many small leaves, whereas thick shoots typically support fewer, bigger leaves (Corner 1949; Westoby & Wright 2003). Moreover, the chemistry of a plant shoot can be reflected by leaf traits, e.g. broad leaves contain more water and needle leaves often contain more volatile components (Rowe & Scotter 1973; Materić *et al.* 2015). Given these links with fire behaviour, shoot architecture and shoot chemistry, leaf traits are expected to influence the burning characteristics of a shoot, and an improved understanding of these relationships would help to upscale from leaf-level functional traits to fire behaviour in different biomes (Schwilk 2015, Archibald *et al.* 2018). Finally, for many species, leaf traits are comparatively easy to measure, and there are extensive data held in large global databases (e.g. TRY; Kattge *et al.* 2011). Therefore, if we can identify quantitative relationships between shoot flammability and leaf morphological and chemical traits, these extensive global trait databases can be unlocked to predict shoot flammability across many species.

We used measurements of leaf functional traits, and leaf- and shoot-level flammability taken across 43 common indigenous perennial New Zealand plant species to i) explore how flammability differs between leaf- and shoot-level measurements for the same species; ii) compare the leaf-level (Mason *et al.* 2016) and shoot-level (Wyse *et al.* 2016) flammability rankings with the flammability of the same species in field conditions as determined by expert opinion (Fogarty 2001); and iii) explore which suites of leaf traits, if any, are correlated with shoot flammability. While a recent study by Ganteaume (2018) compared leaf and litter bed level flammability, to our knowledge, ours is the first study to compare the most commonly used plant flammability measurement (i.e. leaf-level flammability) to an approach (shoot-level flammability) that retains aspects of plant architecture, and which then assesses each approach against independently determined rankings derived from expert opinion of field-based fire behaviour.

2.3 Materials and methods

2.3.1 Species used in this study

To assess plant flammability and its relationships with leaf functional traits, we compiled existing flammability and functional trait data for 43 common indigenous New Zealand plant species across 35 families. Species were chosen based on the availability of both the functional trait and flammability data on the same species. These species comprised twenty-two angiosperm trees, five coniferous trees, five ferns (including three tree ferns), one long-lived forb, one grass, six shrubs, and three lianas. The species were collected from a broad range of habitats on the North, South, and Stewart Islands of New Zealand. Data were obtained using leaves from 10-40 individuals per species for the leaf-level data, and single 70 cm-long shoots from 6-21 individual plants per species for the shoot-level data. For details describing the species and their sampling see Table S2.1, Mason *et al.* (2016), Wyse *et al.* (2016) and Padullés Cubino *et al.* (2018).

2.3.2 Functional trait measurements

We obtained leaf morphological and chemical trait data from Mason *et al.* (2016), or the Manaaki Whenua-Landcare Research Traits Database (https://ecotraits.landcareresearch.co.nz/). In those studies, at least ten fully expanded leaves from each species were used to measure the functional traits (Fig. S2.1, Table S2.3). The leaf area, perimeter, length, and width were measured from digital images (Epson Expression 10000XL scanner) and WinFOLIA Pro V. 2012 software (Regent Instruments Inc., Quebec City). Leaf thickness was measured with callipers, and fresh mass was recorded for all leaves. Leaf volume was calculated by multiplying the leaf area by the thickness and used to calculate leaf surface area to volume ratio (SA:V). The leaves were then oven-dried at 60°C for 48 h to obtain the leaf dry mass (LDM), which was used to calculate specific leaf area (SLA) and leaf dry matter content (LDMC). Among the chemical traits, percent nitrogen (N) and phosphorus (P) were calculated using the acid digest and colorimetric methods of Blakemore *et al.* (1987). The percent acid detergent cellulose (ADC) and percent acid detergent lignin (ADL) were determined using the acid detergent method described by Rowland and Roberts (1994). The percent condensed tannins was calculated using the vanillin method of Broadhurst and Jones (1978) and total phenols were quantified using the method of Price and Butler (1977).

2.3.3 Flammability variable measurements

We collated shoot-level flammability data of 43 plant species from Wyse *et al.* (2016), Padullés Cubino *et al.* (2018) and Donkers, Alam, Bréda, Blackwood, O'Connell and Curran (unpublished data), while the leaf-level flammability data for the same species were obtained from Mason *et al.* (2016). To measure shoot-level flammability, 70 cm-long terminal shoots of woody plants or ferns, and the lower 70 cm parts of herbs or grasses were burnt in the apparatus described by Jaureguiberry *et al.* (2011), as modified by Wyse *et al.* (2016). First, the samples were laid horizontally on the grill on the top of the apparatus, taking care to preserve their natural arrangement. The burners and a blowtorch were positioned below the grill. The burners maintained the grill temperature at c.150°C throughout the burning period, while the blowtorch provided an ignition source for the samples. After preheating samples on the grill for two minutes, the blowtorch was turned on for 10 s to provide the ignition. Measurements started immediately after the blowtorch was turned off. Four flammability variables (ignition percentage, maximum temperature, burn time, and burnt biomass) (Table 2.1) were assessed to characterise flammability of plants at the shoot-level. At least eight individual shoot samples were used in burning for each species with the exception of *Polystichum vestitum* (n = 6) and *Agathis australis* (n = 7) (Table S2.1) (for details see Wyse *et al.* 2016).

To measure leaf-level flammability, single leaves of each plant species were burnt in a muffle furnace (chamber size 380 × 180 × 128 mm) at an oven temperature of 400–430°C, and attached to two thermocouples: one on the hot plate and one at the centre of the oven. At least five individual leaves were burnt from each species, and the entire leaf area was combusted in each burning trial. Leaf temperature was calculated using the thermocouple attached to the centre of the leaf (Mason *et al.* 2016). A data logger (Campbell 21X, Utah, USA) was used to record temperature readings from each of the thermocouples at intervals of 0.5 s. Three flammability variables (Table 2.1) – leaf temperature at smoke production (smoke temperature), leaf temperature at ignition (ignition temperature) and rate of temperature increase from the time of smoke production to maximum recorded leaf temperature (rate of heat release) – were calculated (for details see Mason *et al.* 2016).

Table 2.1 The variables used in this study to assess flammability at both the shoot and leaf levels

Level	Parameter	Measurement method
Shoot	Ignition percentage (%) as Ignitibility	Percentage of sample that ignited during the burning of the sample
	Maximum temperature (°C) as Combustibility	Highest temperature measured during burning of the sample
	Burn time (s) as Sustainability	The duration of flaming combustion
	Burnt biomass (%) as Consumability	Percentage of fuel consumed by fire during burning
Leaf	Ignition temperature (°C) as Ignitibility	Temperature required to ignite the leaf
	Smoke temperature (°C) as Ignitibility	Temperature required to produce smoke from the leaf
	Heat release rate (°C) as Combustibility	Rate of temperature increase from the time of smoke production to maximum temperature

2.3.4 Field-level plant flammability ranking by expert opinion

Flammability rankings based on expert opinion were taken from Fogarty (2001) for a subset of the species. These rankings were derived from a quantitative analysis of ordinal classifications of plant flammability (High, Moderate/High, Moderate, Low/Moderate, Low) based on field observations by 59 fire managers of species' burning characteristics during wildfires or prescribed burns across New Zealand. Forty-two indigenous New Zealand species (mostly trees and shrubs) were ranked using the average flammability score derived from observations by fire managers. Of the 42 species assessed by Fogarty (2001), we retained only those species that were common with our leaf- (n = 28) and shoot-level (n = 31) data.

2.3.5 Data analysis

A principal component analysis (PCA) was conducted, including four shoot-level flammability variables and three leaf-level flammability variables (Table 2.1). This PCA allowed us to examine the relationships between these different flammability variables. A shoot-only PCA and a leaf-only PCA were used to rank species by both shoot and leaf-level flammability based on the first component PCA score at each level (Wyse *et al.* 2016). This component explained the majority of the variation in the data in each level (shoot-level: 83% (Fig. S2.2a) and leaf-level: 77% (Fig. S2.2b)). We used Spearman's rank correlation to compare the flammability ranking based on leaf (28 species) and shoot (31 species) data with the rankings as determined by expert opinion (Fogarty 2001), to understand how the flammability of plants at the leaf and shoot levels correlated with the flammability of plants in the field.

In addition, separate PCAs were conducted using leaf morphological and chemical traits to visualise their covariation across species (Fig. S2.3). All PCAs were performed using the *princomp* function from *stats* package in R version 3.4.1 (R Core Team, 2017) using the correlation matrices of the data as the variables were measured using different units.

Also, the sum of squares data from an analysis of variance (ANOVA) was used to partition variance in each flammability variable into among-species and within-species components.

To explore how the leaf traits were related to the variables of shoot flammability, generalized linear models (GLM) were used to establish the strength and direction of leaf traits contributing to each measured flammability variable. GLMs used a Gamma error distribution with a log link function determined by the distribution of the response variables in quantile-quantile plots. Multicollinearity between the functional traits was assessed using Pearson's correlation coefficient (Fig. S2.1) and variance inflation factors (VIF). VIF was calculated using the function *vif* in the R package *car* (v 3.0-0) (John & Sanford 2011). Due to strong correlations between some traits, we restricted our analyses to nine, uncorrelated traits that maximized the trait variation analysed ($-0.6 < r < 0.6$; VIF < 3) (Zuur *et al.* 2010; Dormann *et al.* 2013). Leaf dimensions were highly correlated, so only leaf length was included in the analysis and leaf width and perimeter were removed. LDM and SLA were included instead of leaf area and SA:V, while leaf phosphorus and phenolics were included, and nitrogen and tannins removed. To allow better comparisons with existing studies, when faced with a choice between two highly correlated traits, we retained the one that had been more widely used in other studies as

a predictor of flammability. All predictor variables were standardized using the *scale* function in R prior to analysis so that parameter estimates were on a comparable scale. For each GLM we calculated the variance function based R-squared values (R^2) (Zhang 2017) using the R package *rsq* (v 1.1) (Zhang 2018) to assess model fit. Due to missing values for some traits, 39 species were included in the GLM analysis. Also, we calculated the Pearson Correlation Coefficients between the leaf traits and shoot flammability variables (Table S2.6). All analyses were performed using functions and routines implemented in the R software package version 3.4.1 (R Core Team, 2017).

2.4 Results

2.4.1 Flammability differences between leaf- and shoot-level

Principal component analysis of the plant flammability data showed that leaf-level flammability variables were orthogonal to shoot-level flammability variables (Fig. 2.1). The first two components of the PCA represented most of the variation (81%) in the data. The first PCA axis explained 49.6% of the variation and was mainly associated with the four shoot flammability variables, whereas the second axis explained 31.6% of the variation and was mainly associated with leaf flammability variables. All shoot-level flammability variables were negatively loaded on PCA axis 1 (ignition percentage: -0.458; maximum temperature: -0.498; burn time: -0.460 and burnt biomass: -0.481), while two of the leaf-level flammability variables had positive (ignition temperature: 0.547 and smoke temperature: 0.592) and the third had negative (rate of heat release: -0.518) loadings on the second axis. At the shoot-level, species with a low PCA score for all four traits on both axes were more flammable, whereas species with a high PCA score for ignition temperature and heat release rate on the first axis and a low PCA score for all three traits on the second axis were more flammable at the leaf-level (Fig. 2.1).

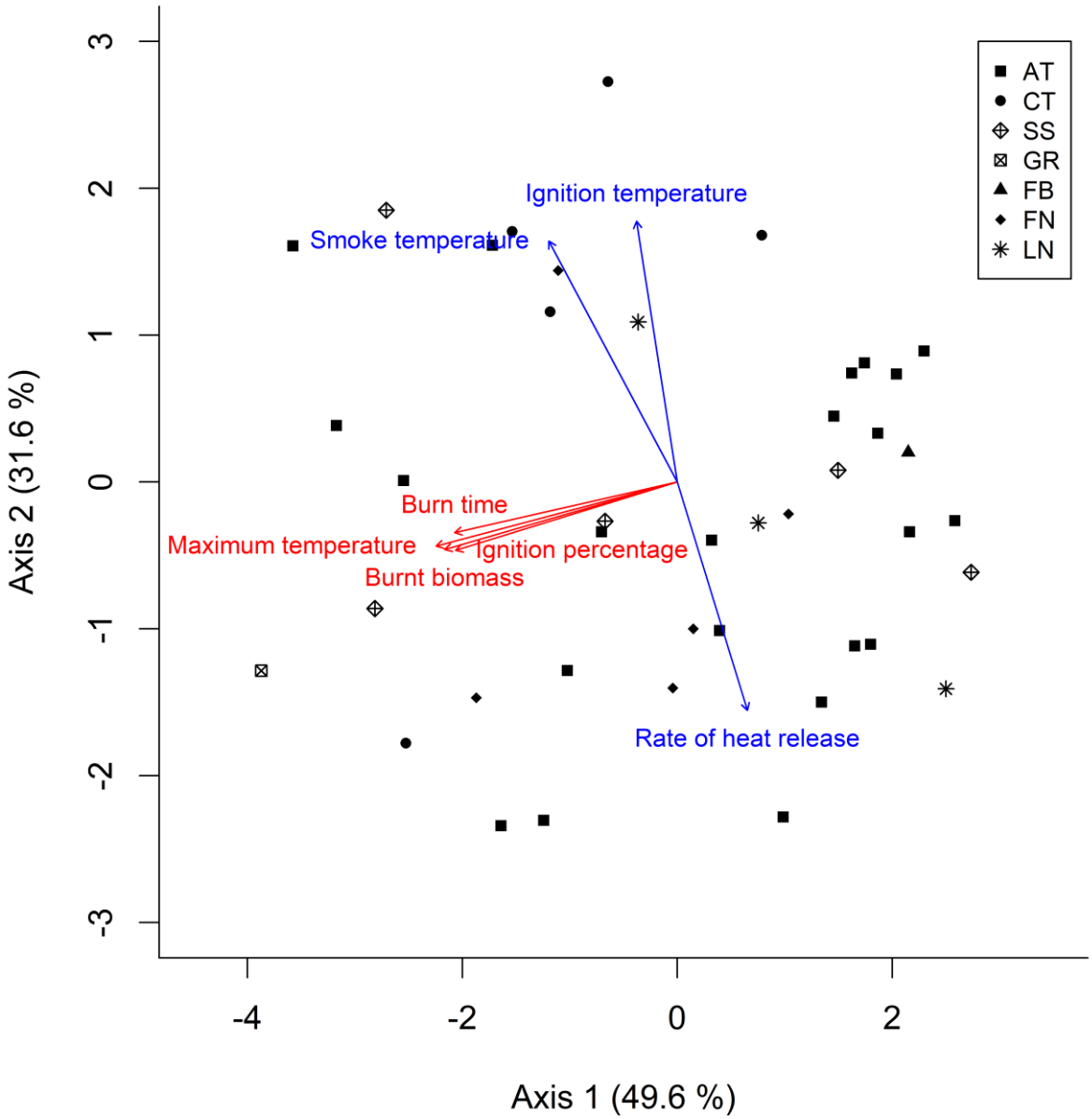

Figure 2.1 Principal component analysis (PCA) of the four shoot-level flammability variables (red vectors: ignition percentage, maximum temperature, burn time and burnt biomass) and three leaf-level flammability variables (blue vectors: ignition temperature, smoke temperature and rate of heat release). Each point is a species mean score. AT- Angiosperm tree, CT- Conifer tree, SS- Shrub, FB- Forb, FN- Fern, GR- Grass, LN- Liane.

2.4.2 Comparing plant flammability at the leaf- and shoot-level to expert opinion at the field

The leaf-level flammability ranking was not correlated with the flammability ranking of plants based on expert opinion derived from field observation (Spearman's $\rho = -0.279$, $P = 0.17$; Fig. 2.2a). However, the flammability ranking at the shoot-level was positively correlated with the flammability ranking of plants based on expert opinion (Spearman's $\rho = 0.70$, $P < 0.0001$; Fig. 2.2b).

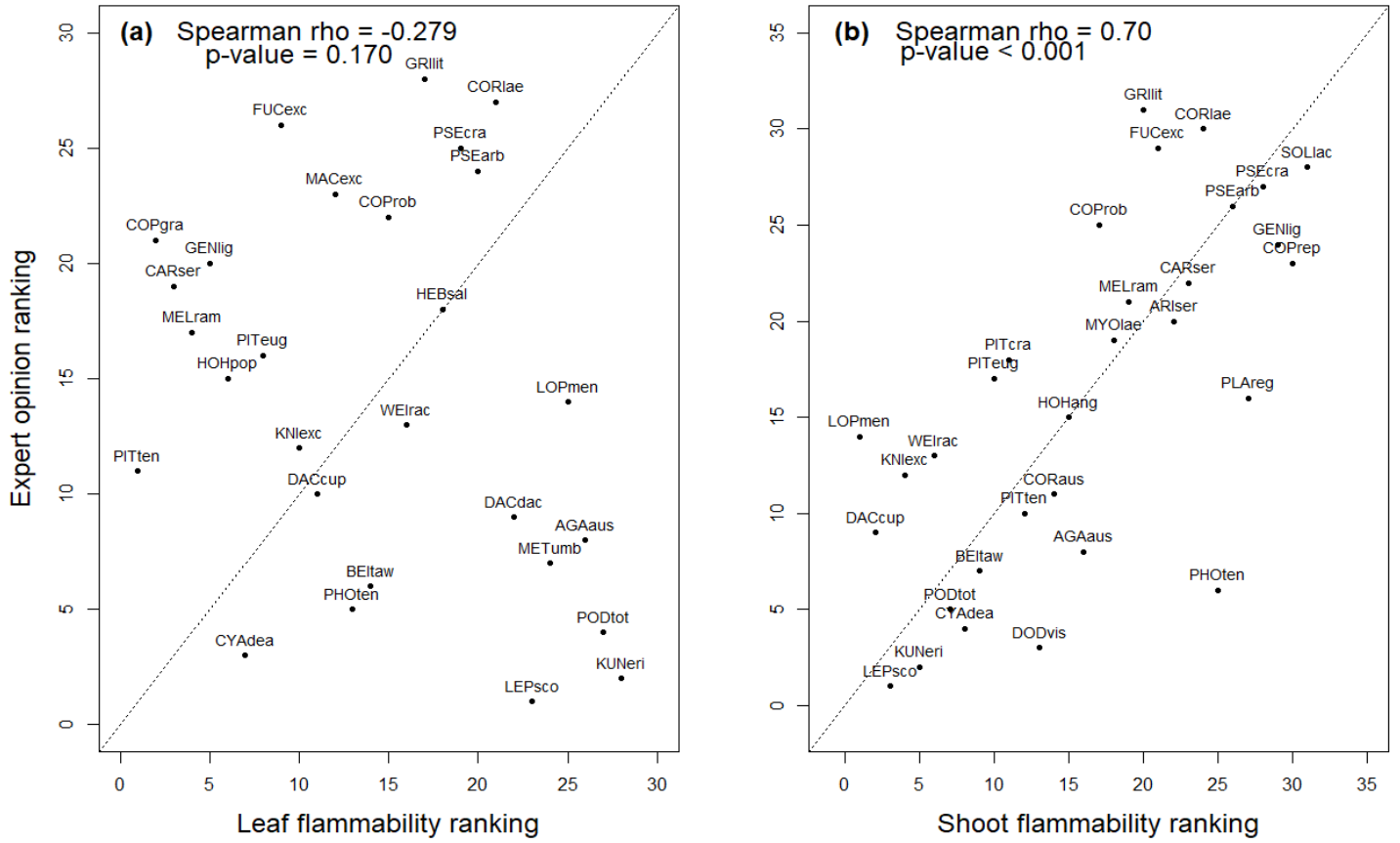

Figure 2.2 Comparison of species flammability rankings derived from both leaf-level (a) and shoot-level (b) data with those determined by Fogarty (2001) using expert opinion. The dashed line indicates where points would lie in a perfect correlation between both ranking systems. Lower numbers indicate higher flammability. See Table S1 for species codes.

2.4.3 Relationships between leaf functional traits and shoot flammability

The proportion of variance in all the shoot flammability variables was found to be higher between (58–68%) than within species (32–42%) (Table S2.5). All four shoot flammability variables were related to leaf functional traits, with a suite of leaf morphological and chemical traits being most associated with shoot-level flammability. The amount of variation explained by leaf traits varied from the highest for combustibility (R^2 = 0.63) to the lowest for consumability (R^2 = 0.41). The leaf traits that significantly contributed to explaining each of the flammability variables were LDMC, leaf thickness, phenolics and lignin (Table 2.2). Overall, among all leaf traits, LDMC was most strongly associated with flammability and showed a positive relationship with all flammability variables (Table 2.2, Fig. 2.3). Plants with high LDMC ignited faster, burnt at a higher temperature, burnt longer, and had greater biomass consumption.

Table 2.2 Contribution of leaf functional traits to shoot flammability as determined by generalized linear models. Values represent coefficient estimates ± SE of the slopes, and *P* values ('**'$P < 0.01$, '*' $P < 0.05$).

Traits	Ignition percentage (%)	Maximum temperature (°C)	Burn time (s)	Burnt biomass (%)
Leaf length	0.031 ± 0.07	0.072 ± 0.05	-0.032 ± 0.17	0.019 ± 0.14
Leaf dry mass	0.026 ± 0.10	0.041 ± 0.08	0.020 ± 0.28	-0.045 ± 0.22
Leaf dry matter content	0.177 ± 0.09 *	0.158 ± 0.07 *	0.567 ± 0.24 *	0.617 ± 0.18 **
Leaf thickness	-0.180 ± 0.08 *	-0.043 ± 0.06	-0.107 ± 0.21	-0.293 ± 0.17
Specific leaf area	-0.071 ± 0.09	-0.15 ± 0.07	0.108 ± 0.24	0.269 ± 0.19
Phosphorus	-0.015 ± 0.06	-0.043 ± 0.04	-0.138 ± 0.17	-0.009 ± 0.13
Phenolics	0.102 ± 0.06	0.123 ± 0.04 *	0.068 ± 0.16	0.197 ± 0.13
Lignin	0.114 ± 0.08	0.209 ± 0.06 **	0.502 ± 0.21 *	0.432 ± 0.17 *
Cellulose	0.017 ± 0.08	-0.016 ± 0.06	-0.045 ± 0.21	-0.104 ± 0.16
R^2	0.48	0.63	0.56	0.41

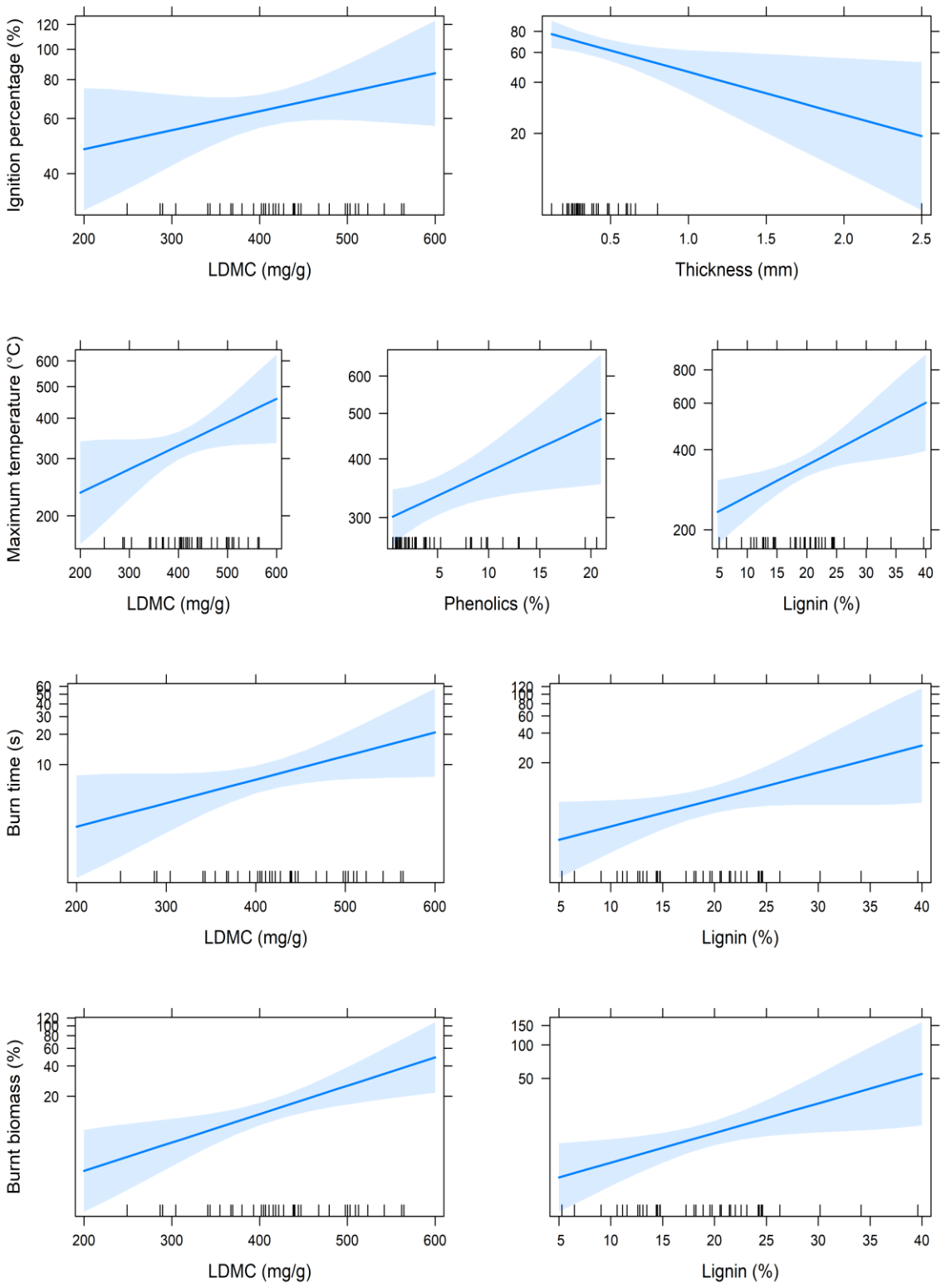

Figure 2.3 Effect plots showing the predicted (blue line) relationship of the shoot flammability variables as a function of the significant leaf functional traits from the generalised linear models. The blue envelope represents the 95% confidence interval. Observed trait data are represented by the small black lines on the *x*-axes. The plots show the relationship between the flammability variables and each of the functional traits in the model where other variables were held constant.

Leaf thickness was another morphological trait negatively related to ignitibility ($P < 0.05$) with thick-leaved plants taking longer to ignite (Table 2.2, Fig. 2.3), although the significant relationship did not hold when the thick-leaved plant (*Phormium tenax*) was excluded from the analysis. In contrast, leaf length, LDM, and SLA made minor contributions to explaining the shoot flammability variables (Table 2.2, Table S2.6).

Lignin was the most important leaf chemical trait and was significantly positively associated with all shoot flammability variables except ignitibility (Table 2.2, Fig. 2.3). Phenolic content was another important chemical trait and had a significant, positive association with combustibility ($P < 0.01$). In contrast, both phosphorus and cellulose were not significantly associated with shoot flammability (Table 2.2).

2.5 Discussion

2.5.1 Plant flammability differs at the leaf and shoot levels

Our study demonstrates that measurements of shoot-level flammability are decoupled from leaf-level flammability, which suggests that care must be taken when comparing plant flammability assessments conducted using different fuel levels. Leaf-level studies are common in fire ecology and fire evolution studies because they are easier to conduct, and leaves are usually the plant component that ignites first and is assumed to drive flammability (Etlinger & Beall 2005; Gill & Zylstra 2005; Pickett *et al.* 2009; Zylstra *et al.* 2016). However, with the increasing importance of obtaining accurate estimates of plant flammability for land management, it is important to understand how leaf-level tests correlate with flammability measurements conducted at larger levels. To our knowledge, this is the first study to quantitatively compare proxies for canopy flammability at two levels across a wide range of species.

The lack of correlation between leaf- and shoot-level flammability is likely to be explained by differences in the amount and arrangement of the fuel being burned. While in leaf-level studies a single leaf is burnt, the shoot-level study uses a 70 cm-long shoot as fuel, which contains multiple leaves, twigs and small branches. The flammability of vegetation is influenced by fuel arrangement, continuity, and quantity (Martin *et al.* 1994), and our results suggest that these principles apply at the shoot-level. The arrangement of leaves and twigs at the shoot-level likely reflects the way that fire burns through a plant canopy, with the propagation of fire from twig to twig on a shoot similar to propagation from branch to branch in a canopy. The burning of

single leaves may be more relevant to litter fires (Varner *et al.* 2015; Grootemaat *et al.* 2017a; Ganteaume 2018), albeit without the more realistic representation of fuel bulk density that comes with burning leaf litter mixes.

Another possible explanation for the decoupling of the leaf- and shoot-level flammability relates to the measurement methods. Leaf flammability was calculated by burning a single leaf in a muffle furnace at an oven temperature of 400–430°C, without applying any ignition source (Mason *et al.* 2016), as has been done in several other studies (Montgomery & Cheo 1971; Murray *et al.* 2013; Krix & Murray 2018; Krix *et al.* 2019). Exposing the leaf to such high temperatures in the absence of a flame is likely to remove any volatile oils present in the leaf before they ignite, and thus overestimate the ignition time of a leaf. Leaf volatile organic compounds (VOCs; e.g. tannins, terpenes, isoprenoids, and phenolics) increase plant flammability (Owens *et al.* 1998; Alessio *et al.* 2008; Chetehouna *et al.* 2009; Pausas *et al.* 2016), and phenolic concentrations were positively correlated with shoot-flammability in our study. Species with high VOCs are likely to be slow to ignite unless a flame is used (Martin *et al.* 1994), suggesting that methods that use an ignition source are better suited to measuring the ignitibility of these species.

These potential differences in measurement methods could be resolved by direct comparisons of leaf-level tests in a muffle furnace with and without an ignition source, but we could find no such studies (see text in SI, Table S2.4). However, we can indirectly compare results with and without an ignition source by assessing whether different methods produced similar relationships between leaf traits and flammability. In doing so, we found similar trait-flammability relationships between the methods (Table S2.4). This provides support for the contention that the leaf flammability measured in a muffle furnace is similar whether or not an ignition source is used. Thus, we conclude that the lack of correlation between shoot and leaf flammability in our study was unlikely to be due to methodological differences (absence of an ignition source), but recommend direct tests of this for confirmation.

Given that the level of the fuel material influences measurements of flammability, which level best represents whole-plant and potentially ecosystem flammability? Ultimately, addressing this question requires burning whole plants in the laboratory and plant communities in the field and comparing the results to predictions of fire behaviour based on tests on plant components. However, our finding that shoot-level, but not leaf-level flammability, rankings were correlated with rankings by experts suggests that shoot-level tests will upscale better than leaf-level tests

to whole plant or ecosystem flammability. In his instructions to respondents of his expert survey, Fogarty (2001) asked fire managers to isolate the flammability of the species they were assessing from that of the vegetation that was burning and to pay particular attention to how well species burnt in a head fire or during high-intensity burn-offs. This focussed questioning of a substantial pool of experts (n = 59) lends credence to the findings of that study. However, as Fogarty (2001) acknowledged, further empirical testing in the laboratory and the field is needed to confirm his findings.

2.5.2 Shoot flammability is related to leaf functional traits, including LDMC, leaf thickness, and lignin and phenolic concentrations

Leaf traits explained a substantial proportion of variation in shoot flammability variables (48%, 63%, 56%, and 41% for ignitibility, combustibility, sustainability, and consumability, respectively), with the four most important traits (individually and in combination) being LDMC, leaf thickness, lignin content, and phenolic content. LDMC was the leaf trait most strongly correlated with shoot flammability and was positively related to all four traits of shoot flammability, suggesting that higher dry matter content resulted in higher flammability. This result confirms the suggestion in the standardised trait measurement handbooks that LDMC is an important trait positively related to flammability (Cornelissen *et al.* 2003; Perez-Harguindeguy *et al.* 2013). LDMC is closely related to the water content and tissue density of the leaves. High dry matter content indicates low water content and high dry mass per volume of the tissue (Garnier & Laurent 1994; Wilson *et al.* 1999; Shipley & Vu 2002; Perez-Harguindeguy *et al.* 2013). Hence, the higher shoot flammability of the species with high LDMC content in this study was likely due to the low water content of the leaves, which therefore require less energy to combust (Pompe & Vines 1966; Chuvieco *et al.* 2009). Additionally, the higher available dry tissue mass per volume allows the fuels to ignite more rapidly, burn with higher intensity for longer, and causes higher biomass consumption (Dimitrakopoulos & Papaioannou 2001; Chuvieco *et al.* 2004; De Lillis *et al.* 2009; Cowan & Ackerly 2010; Perez-Harguindeguy *et al.* 2013). LDMC is a trait that is relatively easy to measure and is widely available in global trait databases (e.g. Kleyer *et al.* 2008; Kattge *et al.* 2011; Tavşanoğlu & Pausas 2018), potentially making it a useful predictor of plant flammability.

Leaf thickness was another morphological trait related to shoot-level flammability, with thick-leaved plants igniting more slowly. Leaf-level experiments have demonstrated that thicker leaves take longer to ignite and release less heat during burning, contributing to the fire retardance of plants (Montgomery & Cheo 1971; Grootemaat *et al.* 2015; Mason *et al.* 2016). However, such findings are not universal; Murray *et al.* (2013) found no relation between leaf thickness and leaf flammability. Interestingly, leaf thickness was the only trait that reduced ignitibility at both the shoot- and leaf-level in our study, although these two levels of flammability were orthogonal. This may be because leaves are the first component to ignite during fire irrespective of the fuel levels and suggests that ignitibility is influenced by leaf thickness at any fuel level. While this finding matches that of most other studies, we recommend that it be treated cautiously, as the significant negative relationship between ignitability and leaf thickness in our study is mostly driven by the thick-leaved perennial herb *Phormium tenax*.

Lignin content of leaves was the chemical trait most strongly correlated with shoot flammability, with flammability increasing with leaf lignin content. Tissues with high lignin content have low water storage capacity (Berry & Roderick 2005) and high energy content (Hough 1969; Demirbas 2002; McKendry 2002) and burn hotter and longer after ignition (Fernandes 2013). Although lignin reduces tissue combustibility at the pyrolysis stage (Grootemaat *et al.* 2015; Xu & Ferdosian 2017), once lignin-rich tissue ignites it intensifies the fire, producing high temperatures due to its high energy content. Phenols were also correlated with shoot flammability: plant species with high phenolic compound concentrations had higher combustibility at the shoot-level. Phenolic compounds (flavonoids, phenolic acids, tannins, terpenes) are often produced in plants during stress (Ormeno *et al.* 2007; Fernandes 2013). Phenols are strongly positively related to plant flammability in several other studies (White 1994; Owens *et al.* 1998; Ormeno *et al.* 2009; Keith 2012) because fuels high in phenolic compounds have high calorific values (Núñez-Regueira *et al.* 2002, 2005), which makes them burn more intensely.

Collectively, these trait correlations demonstrate how different leaf morphological and chemical traits influence shoot flammability and highlight the significance of considering leaf functional traits to explain shoot flammability. Although several of the leaf traits we evaluated contribute to shoot flammability, LDMC is clearly the most important. While leaf-level traits were related to shoot flammability, architectural traits (e.g. spatial arrangement of leaves and twigs, branch ramification, and retention of dead material) are also likely to influence shoot-level flammability (Schwilk 2003; Perez-Harguindeguy *et al.* 2013). However, none of these

measurements currently exist for our study species. Future studies should examine whether architectural traits are more important drivers of shoot flammability than leaf traits.

2.6 Conclusion

Our study demonstrates the importance of fuel level when measuring plant flammability and shows for the first time that leaf- and shoot-level flammability is decoupled. This decoupling suggests that caution is needed when leaf-level measurements are scaled up to predict the flammability of larger plant components or fire behaviour. For the species that we considered, shoot-level flammability was highly correlated with plant-level flammability, as determined by expert opinion based on field observations, and hence is likely a useful way to characterize plant flammability. However, shoot flammability research is in its infancy, with only several hundred species (ca 400) tested so far globally (Jaureguiberry *et al.* 2011; Burger & Bond 2015; Calitz *et al.* 2015; Wyse *et al.* 2016; Padullés Cubino *et al.* 2018). Thus, there is a need to identify widely measured traits that could be used as a surrogate for shoot-level flammability. To this end, our study has identified several key leaf traits (LDMC, thickness, phenolics, and lignin) that are strongly correlated with shoot flammability. Some of these traits (e.g. LDMC with 4941 species entries in the TRY trait database (Kattge *et al.* 2011) and 1735 species in the LEDA trait database (Kleyer *et al.* 2008)) have been widely measured globally. Assuming the relationships described here hold when more coniferous trees and deciduous trees are assessed, LDMC could act as a surrogate for the shoot- and perhaps plant-level flammability in global dynamic vegetation models, facilitating improved modelling of fire-climate-vegetation feedbacks associated with global change.

2.7 Supplementary Information

Figure S2.1 Pairs plots for the leaf functional traits

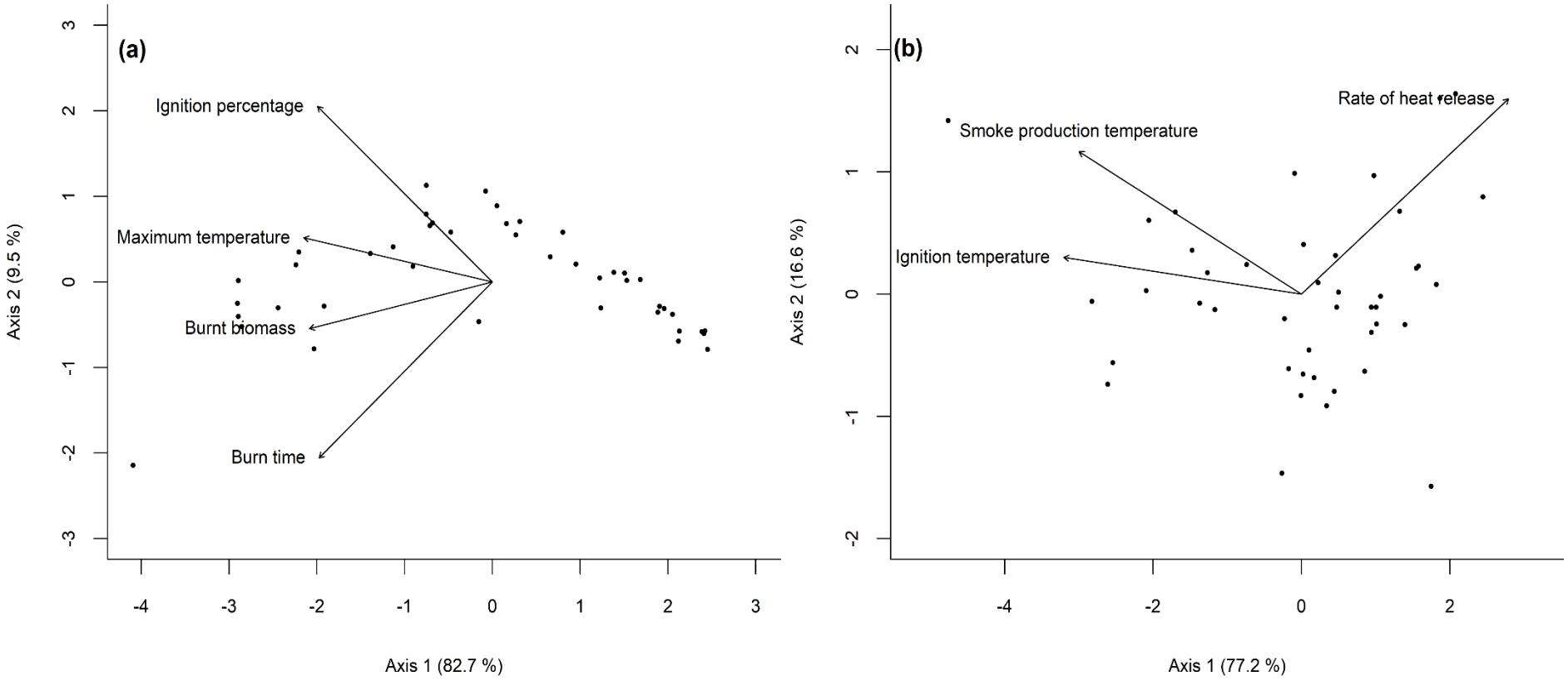

Figure S2.2 Principal component analysis (PCA) of shoot-level (a) and leaf-level (b) flammability measurements

Supplementary text: Variation among species in leaf functional traits

The first axis of the PCA of leaf morphological traits (Fig. S2.3a) explained 44% of the variation and was negatively related to leaf length, width, area, perimeter, thickness and leaf dry mass, and positively related to SA:V. The second axis of this PCA explained a further 24% of the variation in the data-set, and was negatively correlated with leaf thickness and LDMC, and positively correlated with SLA (Table S2.2). The first axis of the PCA of leaf chemical traits (Fig. S2.3b) explained 35.4% of the variation and was negatively correlated with percent nitrogen and phosphorus, and positively correlated with lignin content. The second axis explained a further 28% variation in foliar chemical data, and was negatively correlated with leaf phenolics and tannins and positively correlated with cellulose content (Table S2.2).

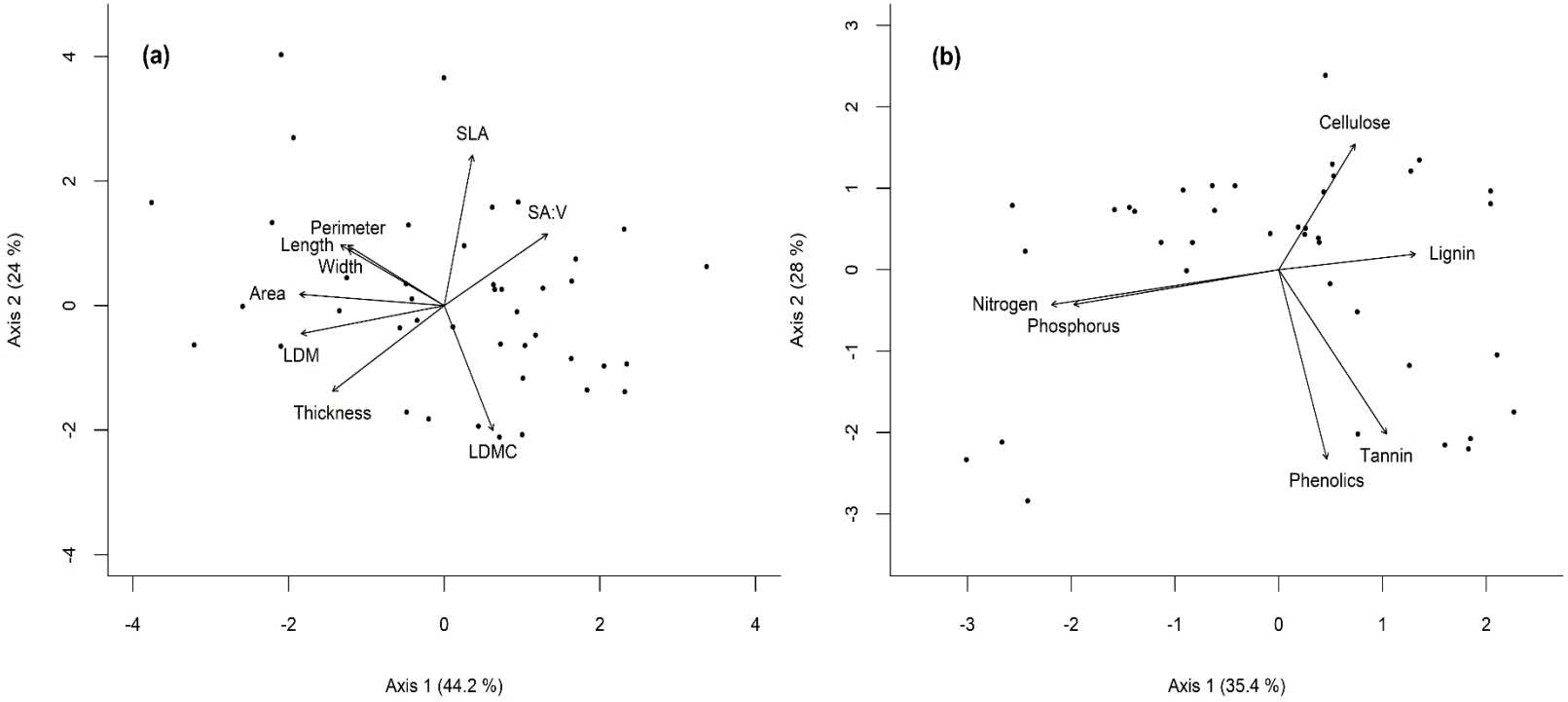

Figure S2.3 Principal component analysis (PCA) of leaf morphology traits (a) and leaf chemical traits (b)

Table S2.1 Plant species included in this study. Taxonomy follows the New Zealand Plant Conservation Network (see: http://www.nzpcn.org.nz)

Species	Code	Family	Structural type	Leaf (n)	Shoot (n)
Kauri (*Agathis australis* (D.Don) Lindl. ex Loudon)	AGAaus	Araucariaceae	CT	10	7
Tītoki (*Alectryon excelsus* Gaertn.)	ALEexc	Sapindaceae	AT	10	8
Tawa (*Beilschmiedia tawa* (A.Cunn.) Benth. and Hook.f. ex Kirk)	BEItaw	Lauraceae	AT	20	8
Marble Leaf (*Carpodetus serratus* J.R.Forst & G.Forst.)	CARser	Grossulariaceae	AT	20	8
Māmāngi (*Coprosma arborea* Kirk)	COParb	Rubiaceae	SS	10	8
Mingimingi (*Coprosma propinqua* A.Cunn.)	COPpro	Rubiaceae	SS	10	8
Karamū (*Coprosma robusta* Raoul)	COProb	Rubiaceae	AT	20	8
Karaka (*Corynocarpus laevigatus* J.R.Forst. and G.Forst.)	CORlae	Corynocarpaceae	AT	10	8
Ponga (*Cyathea dealbata* (G.Forst.) Sw.)	CYAdea	Cyatheaceae	TF	10	8
Mamaku (*Cyathea medullaris* (G.Forst.) Sw.)	CYAmed	Cyatheaceae	TF	10	8
Rimu (*Dacrydium cupressinum* Lamb.)	DACcup	Podocarpaceae	CT	20	8
Whekī (*Dicksonia squarrosa* (G.Forst.) Sw.)	DICsqu	Dicksoniaceae	TF	20	8
Matagouri (*Discaria toumatou* Raoul)	DIStou	Rhamnaceae	SS	20	17
Inaka (*Dracophyllum longifolium* J.R.Forst., G.Forst.)	DRAlon	Epacridaceae	SS	20	8
Kohekohe (*Dysoxylum spectabile* (G.Forst) Hook.f.)	DYSspe	Meliaceae	AT	10	8
Hard tussock (*Festuca novae-zelandiae* (Hack.) Cockayne)	FESnov	Poaceae	GR	10	8
Kōtukutuku (*Fuchsia excorticata* (J.R.Forst. and G.Forst.) L.f.)	FUCexc	Onagraceae	AT	20	8
Mountain Beech (*Fuscospora cliffortoides* (Hook.f.) Heenan and Smissen)	FUScli	Nothofagaceae	AT	20	8
Red Beech (*Fuscospora fusca* (Hook.f.) Heenan and Smissen)	FUSfus	Nothofagaceae	AT	40	8
Silver Beech (*Lophozonia menziesii* (Hook.f.) Heenan and Smissen)	LOPmen	Nothofagaceae	AT	30	8
Hangehange (*Geniostoma ligustrifolium* A.Cunn.)	GENlig	Loganiaceae	SS	10	18
Broadleaf (*Griselinia littoralis* Raoul)	GRIlit	Cornaceae	AT	30	8
Rewarewa (*Knightia excelsa* R.Br.)	KNIexc	Proteaceae	AT	20	21

Kānuka (*Kunzea ericoides* (A.Rich) Joy Thomps. sensu lato.)	KUNeri	Myrtaceae	AT	20	8
Mānuka (*Leptospermum scoparium* J.R.Forst. and G.Forst.)	LEPsco	Myrtaceae	AT	20	9
Soft mingimingi (*Leucopogon fasciculatus* (G.Forst.) A.Rich.)	LEUfas	Epacridaceae	SS	20	8
Māhoe (*Melicytus ramiflorus* J.R.Forst. and G.Forst.)	MELram	Violaceae	AT	20	9
Rata (*Metrosideros fulgens* Sol. ex Gaertn.)	METful	Myrtaceae	LN	10	8
Pohuehue (*Muehlenbeckia australis* (G.Forst.) Meisn)	MUEaus	Polygonaceae	LN	10	12
Māpou (*Myrsine australis* (A.Rich.) Allan)	MYRaus	Myrsinaceae	AT	30	8
Harakeke (*Phormium tenax* J.R.Forst. and G.Forst.)	PHOten	Xanthorrhoeaceae	FB	10	8
Tanekaha (*Phyllocladus trichomanoides* D.Don)	PHYtri	Phyllocladaceae	CT	40	8
Tarata (*Pittosporum eugenioides* A.Cunn)	PITeug	Pittosporaceae	AT	20	9
Kohuhu (*Pittosporum tenuifolium* Sol. ex Gaertn.)	PITten	Pittosporaceae	AT	20	20
Tōtara (*Podocarpus totara* G.Benn. ex D.Don)	PODtot	Podocarpaceae	CT	10	8
Punui (*Polystichum vestitum* (G. Forst.) C. Presl)	POLves	Dryopteridaceae	FN	10	6
Miro (*Prumnopitys ferruginea* (D.Don) de Laub.)	PRUfer	Podocarpaceae	CT	10	8
Five-finger (*Pseudopanax arboreus* (Murray) Philipson)	PSEarb	Araliaceae	AT	30	13
Red horopito (*Pseudowintera colorata* (Raoul) Dandy)	PSEcol	Winteraceae	AT	20	12
Lancewood (*Pseudopanax crassifolius* (Sol. ex A.Cunn.) C.Koch)	PSEcra	Araliaceae	AT	10	8
Bracken (*Pteridium esculentum* (G.Forst.) Cockayne)	PTEesc	Dennstaedtiaceae	FN	10	8
Tataramoa (*Rubus cissoides* A.Cunn.)	RUBcis	Rosaceae	LN	20	9
Kāmahi (*Weinmannia racemosa* L.f.)	WEIrac	Cunoniaceae	AT	30	8

AT-Angiosperm tree, CT-Conifer tree, SS-Shrub, FB-Forb, GR-Grass, FN-Fern, TF-Tree fern, LN-Liane
n- Number of samples used to take measurements at the leaf- and shoot-level

Table S2.2 Factor loadings from the principal component analysis (PCA) of shoot flammability variables, leaf morphological and chemical traits of studied species.

Level	Variables	Axis 1	Axis 2
Shoot flammability	Ignition percentage	-0.49	0.68
	Maximum temperature	-0.52	0.17
	Burn time	-0.48	-0.68
	Burnt biomass	-0.51	-0.18
	% Variance	82.70	9.50
Leaf morphology traits	Length	-0.39	0.17
	Width	-0.38	0.19
	Area	-0.50	
	Perimeter	-0.39	0.15
	Thickness	-0.35	-0.40
	LDM	-0.46	-0.11
	LDMC	0.23	-0.47
	SLA		0.63
	SA.V	0.36	0.36
	% Variance	40.00	26.40
Leaf chemical traits	Nitrogen	-0.63	-0.12
	Phosphorus	-0.56	-0.12
	Phenolics	0.13	-0.66
	Tannins	0.30	-0.58
	Cellulose	0.21	0.44
	Lignin	0.38	
	% Variance	35.40	27.80

Table S2.3 Ranges of values for all the leaf functional traits used in the analysis in this study

Functional trait	Minimum	Maximum	Mean
Leaf length (mm)	5.58	142.45	53.61
Leaf width (mm)	3.30	90.60	27.45
Leaf area (mm)	11	9016	1161
Leaf thickness (mm)	0.12	2.50	0.39
Leaf perimeter (mm)	18.10	605.20	174.10
Leaf dry mass (g)	0.0012	1.3133	0.1569
Leaf dry matter content (mg/g)	158.30	613.40	418.60
Specific leaf area (cm^2/g)	23.26	261.98	93.05
Surface area/volume (mm^{-1})	0.40	8.10	3.31
Leaf nitrogen (%)	0.67	3.81	1.45
Leaf phosphorus (%)	0.04	0.35	0.13
Leaf phenolics (%)	0.63	20.50	5.48
Leaf tannin (%)	0.17	8.19	1.99
Leaf lignin (%)	5.28	39.61	18.66
Leaf cellulose (%)	10.49	38.27	19.54

Supplementary text: Is lack of correlation between leaf- and shoot-level flammability to be explained by differences in the measurement methods?

Ours is the first study to compare the leaf-level and shoot-level tests on the same species, so there are no other studies to directly draw on to tackle this issue. Furthermore, none of the leaf-level studies has compared differing methodological approaches using the same species, so we lack a direct comparison of muffle furnace studies with and without an ignition source. This leaves only an indirect comparison using the results of tests of trait-flammability relationships among studies: i.e. do different techniques yield different relationships between traits and flammability variables?

Muffle furnaces are commonly used in flammability studies to burn single leaves with or without an additional ignition source (Table S2.4). In our study, we used leaf-level flammability data from Mason *et al.* (2016), who used a muffle furnace without an ignition source. Mason *et al.* (2016) calibrated their muffle furnace using tests on filter paper as a standard fuel source, as is common practice (Gill & Moore 1996). With the exception of having an ignition source, Mason *et al.* (2016) modelled their approach on that of Gill & Moore (1996), the methods of which have been used by several other papers using muffle furnaces (Murray *et al.* 2013; Grootemaat *et al.* 2015; Krix & Murray 2018; Krix *et al.* 2019).

However, the question is whether burning leaves with or without an ignition source affects leaf flammability? Here, we have compiled the trait-flammability relationships of plants from different studies which used a muffle furnace for burning (Table S2.4). Overall, leaf-level trait-flammability relationships using muffle furnace have been consistent whether an ignition source is used or not. Among the morphological traits, leaf thickness, leaf area, specific leaf area, and leaf surface area to volume ratio have shown the same relationship with flammability variables irrespective of the ignition source. The negative relationship between leaf thickness and ignitibility of Mason *et al.* (2016) (no ignition source) and Montegomery & Cheo (1971) (no ignition source) was consistent with Grootemaat *et al.* (2015) and Ganteaume (2018), who both had an ignition source. Also, the positive relationship between leaf area and ignitibility of Mason *et al.* (2016), Murray *et al.* (2013) and Krix & Murray (2018) (no ignition source) was the same as Grootemaat *et al.* (2015). Similarly, a positive relationship was found between specific leaf area and ignitibility using a muffle furnace without an ignition source by Mason *et al.* (2016) and Murray *et al.* (2013), which was consistent with the findings of Grootemaat *et al.* (2015) and Ganteaume (2018). Moreover, the positive relationship between the surface area

to volume ratio and ignitibility of Montegomery & Cheo (1971) was consistent with Grootemaat *et al.* (2015) and Gill & Moore (1996) (with ignition source).

There were some differences in trait relationships for studies that looked at LDMC, leaf N, leaf P, tannin, and lignin (Table S2.4), as Grootemaat *et al.* (2015), using an ignition source, found no relationship between these traits and ignitability, whereas Mason *et al.* (2016) found significant trait-ignitability relationships. This could be interpreted as the presence of an ignition source influencing the relationship between leaf chemical traits and ignitability. However, given there is only one study with an ignition source and one study without, it is prudent to resist attributing these differences solely to the presence of an ignition source. For instance, the choice of species in either study could be important: Grootemaat *et al.* (2015) predominantly sampled species from sclerophyllous (where small, thick-leaved species dominate) forest communities in Australia, whereas Mason *et al.* (2016) sampled from a wide range of plant communities in New Zealand (forest, shrubland, grassland).

In summary, although we do not have any direct comparison between muffle furnace studies with and without an ignition source, this evidence from trait-flammability relationships supports the contention that leaf flammability measured in a muffle furnace is similar whether an ignition source is used or not. This is particularly the case for traits which have been examined by several different studies. Consequently, we feel that the flammability testing conducted by Mason *et al.* (2016) provides a suitable representation of other leaf-level tests, thus allowing our main conclusion, that leaf flammability is decoupled from shoot flammability, and that this is likely due to differences in amount and arrangement of fuel, to stand. Furthermore, the varying relationships between traits and measurements of flammability at both levels suggest that the processes governing leaf-level and shoot-level flammability are quite different. While leaf flammability solely reflects the intrinsic fuel properties of leaves, shoot flammability describes how leaves or branches are arranged as well as interactions between the other fuel classes present (live and dead leaves, twigs, and bark).

Table S2.4 Studies showing trait-flammability relationship conducted at leaf-level using muffle furnace with (blue font) or without (black font) ignition source. The bolded values are from Mason *et al.* (2016), which provided the leaf flammability data for the current study.

Functional Traits	Leaf-level flammability variables		
	Ignitability	Combustibility	Sustainability
Leaf length	+ (1), ns (3)		+ (3)
Leaf width	+ (1), ns (3)		+ (3)
Leaf thickness	ns (1), - (3,**4**,5, 7)	- (4),	ns (3)
Leaf area	+ (1,2,3,**4**)	+ (2,4)	+ (2,3), - (7)
Specific leaf area	+ (1,3,7,**4**)		ns (3), +(7)
Leaf SA:V	+ (3,5,6)		
Leaf MC	ns (1), - (2,3,6)	ns (2)	ns (2,3)
LMA	- (2, **4**)	+ (2)	+ (2)
LDMC	ns (3), - (**4**)	- (4)	+ (2)
Leaf N	ns (3), + (**4**)		- (3)
Leaf P	ns (3), + (**4**)		- (3)
Tannin	ns (3), - (**4**)	ns (4)	+ (3)
Lignin	ns (3), - (**4**)	ns (4)	ns (3)

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Table S2.5 Partitioned variance (%) for each of the shoot-level flammability variables at species and individual level calculated from Analysis of Variance (ANOVA)

Flammability variables	% variance explained	
	Species	Individual
Maximum temperature	0.58	0.41
Burn time	0.62	0.37
Burnt biomass	0.68	0.32

Table S2.6 Pairwise Pearson correlation co-efficients between all leaf traits and flammability variables.

Functional traits	Flammability variable			
	Ignition percentage (%)	Maximum temperature (°C)	Burn time (s)	Burnt biomass (%)
Leaf length (mm)	-0.41**	-0.30	-0.23	-0.35*
Leaf width (mm)	-0.33*	-0.31*	-0.35*	-0.33*
Leaf area (mm)	-0.47**	-0.36*	-0.34*	-0.38*
Leaf thickness (mm)	-0.27*	-0.11	-0.12	-0.21
Leaf perimeter (mm)	-0.24	-0.12	-0.19	-0.21
Leaf dry mass (g)	-0.21	-0.23	-0.24	-0.32*
Leaf dry matter content (mg/g)	0.57***	0.64***	0.40**	0.55***
Specific leaf area (cm^2/g)	-0.27	-0.39*	-0.19	0.12
Surface area/volume (mm^{-1})	0.30*	0.09	0.15	0.32*
Leaf nitrogen (%)	-0.18	-0.29	-0.05	-0.03
Leaf phosphorus (%)	-0.19	-0.22	-0.10	-0.03
Leaf phenolics (%)	0.32*	0.35*	0.23	0.33*
Leaf tannin (%)	0.47**	0.55***	0.51***	0.54***
Leaf lignin (%)	0.53***	0.64***	0.55***	0.55***
Leaf cellulose (%)	0.03	0.09	0.06	-0.06

***statistical significance ($P < 0.001$), ** statistical significance ($P < 0.01$), * statistical significance ($P < 0.05$).

Chapter 3

Scaling from functional traits to flammability: leaf traits and fuel architecture determine shoot-level plant flammability

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Author contributions

This study was conceived by TC, AA, GP, and SW and designed by AA, TC, GP, SW, and HB. Samples were collected by AA and XC. Analyses were conducted by AA, TC, HB, SW, JS, and GP. AA wrote the first draft, which was then revised and approved by all co-authors.

3.1 Abstract

1. Flammability is a critical plant characteristic that describes the ability of a plant to burn when exposed to fire. It varies widely among species and can influence the intensity and severity of wildfires. Plant flammability is strongly influenced by functional traits, but the quantitative characterization of trait-flammability relationships has mainly been limited to small plant components (e.g. leaves). This has meant that the influence of architectural traits on flammability has rarely been assessed, which limits our ability to scale up flammability from plant components and functional traits to the whole plants. Shoots preserve some of the architecture of plants, therefore, shoot-level trait-flammability relationships offer great promise in up-scaling from functional traits to whole-plant flammability.

2. We burnt 70 cm shoot samples from 65 indigenous and exotic New Zealand trees and shrub species and measured a range of leaf and architectural traits to 1) examine the effect of leaf and architectural traits on shoot flammability; and 2) predict shoot flammability from functional traits.

3. Shoot flammability was strongly related to both leaf and architectural traits. Leaf dry matter content (LDMC) was the most important functional trait positively associated with shoot flammability, and leaf thickness and specific leaf area were significantly negatively associated with shoot flammability. Architectural traits, such as branching pattern (number of ramifications and sub-branches), were strongly positively correlated with shoot flammability. Other architectural traits, such as foliage and twig fraction mass, and fuel bulk density were also significantly associated with shoot flammability. The full model including all leaf and architectural traits best predicted shoot flammability among all the models.

4. Our study demonstrates that leaf and architectural traits are strongly associated with shoot-level flammability, and species with high LDMC, thin leaves, low SLA, and high levels of branching, twig and foliage mass and fuel bulk density are more flammable. This suggests that these traits can be used as surrogates of plant flammability, and can be used to improve global dynamic vegetation models and fire behaviour models. However, flammability is a complex plant characteristic that requires data from a wide range of traits for appropriate prediction, including easily-measured leaf traits and

difficult-to-measure architectural traits. For this reason, it may be most efficient to simply measure shoot flammability when the aim is to predict whole plant flammability.

3.2 Introduction

Flammability is a complex plant trait that is measured by quantifying several parameters: ignitibility (how fast the fuel ignites), combustibility (how much heat is released during burning), sustainability (how long the fuel continues to burn) and consumability (how much fuel is consumed in the fire) (Anderson 1970; Martin *et al.* 1994; White & Zipperer 2010). Characterising and comparing flammability is complicated due to the use of different plant components and varying methodology of burning (White & Zipperer 2010; Alam *et al.* 2019). While burning single leaves or leaf litter in a fuel bed are the most common ways of measuring flammability (Ganteaume *et al.* 2013b; Murray *et al.* 2013; Grootemaat *et al.* 2015; Krix *et al.* 2019), laboratory-based flammability measurements using small plant components have been criticized because they do not adequately represent plant architecture (Fernandes & Cruz 2012). However, burning plant shoots in the laboratory is rapidly becoming recognised as a standard way of characterizing plant flammability that preserves plant architecture (Perez-Harguindeguy *et al.* 2013; Schwilk 2015), and Alam *et al.* (2019; *Chapter 2*) showed that shoot flammability measurements better represent the flammability of plants as ranked by experts than do leaf flammability measurements. Thus, shoot-level flammability measurements are a promising way to estimate species and ecosystem flammability, which could bridge the gap between laboratory-based flammability assessments conducted on smaller plant components, and fire behaviour in the field. A better understanding of shoot flammability will also improve our knowledge of canopy flammability, a hitherto poorly studied aspect of ecosystem flammability. A plant shoot consisting of multiple leaves and twigs is also likely to be a useful surrogate for canopy flammability, where the fire burns through the adjacent leaves and branches (Alam *et al.* 2019).

Flammability is influenced by plant functional traits. Plant functional traits are those morphological, physiological, and phenological characteristics that determine the response of plants in particular environmental conditions (Perez-Harguindeguy *et al.* 2013). Leaf-level trait-flammability relationships are well studied, and attempts have been made to scale up leaf traits to plant, and ecosystem fire behaviour (Schwilk & Caprio 2011; Zylstra *et al.* 2016), as the leaf is one of the first portions that ignite during a fire (Midgley *et al.* 2011; Murray *et al.* 2013). Leaf flammability is mainly influenced by leaf-level morphological and chemical traits

(Murray *et al.* 2013; Grootemaat *et al.* 2015; Mason *et al.* 2016; Pausas *et al.* 2016), whereas flammability at larger fuel scales is likely controlled not only by leaf traits but also fuel architecture. Plant geometry or architectural traits describe the spatial arrangement and connectivity of the fuel and mainly influence the flammability of large-level fuels (i.e. branch or whole plant), which is crucial to understanding fire behaviour of vegetation (Papió & Trabaud 1990; Schwilk 2003; Perez-Harguindeguy *et al.* 2013; Burger & Bond 2015). Although leaf morphological and chemical traits are often studied to understand the drivers of flammability, plant architectural traits are rarely considered in laboratory studies, due to the need to burn larger fuels.

While leaf-level trait-flammability studies improve our understanding of the intrinsic burning properties of a leaf, studying the influence of plant architecture will advance our knowledge of how fire spreads through leaves and along limbs with varying branching patterns, providing new insights into crown fire behaviour (Papió & Trabaud 1991; Menning & Stephens 2007; Blauw *et al.* 2017). Species with highly branched canopies and tightly spaced leaves and twigs, promote the intensity and spreading of fire by allowing efficient heat transfer (Saura-Mas *et al.* 2010; Schwilk 2015). By preserving plant architecture, shoot-level flammability studies provide the opportunity to quantify the influence of both leaf traits and fuel architectural traits on plant flammability. From this, we can develop predictive models of flammability using both leaf and architectural traits, which can then contribute to the refinement of global dynamic vegetation models used to study fire behaviour globally. If it can be demonstrated that easy-to-measure leaf traits, such as leaf dry matter content or leaf thickness, which have been sampled for many species globally (Kattge *et al.* 2011), are useful predictors of shoot flammability, then those traits could be included in global plant flammability models.

Although shoot-level flammability measurements have been used to study fire behaviour, ecology and plant evolution in different biomes worldwide (Jaureguiberry *et al.* 2011; Burger & Bond 2015; Calitz *et al.* 2015; Wyse *et al.* 2016; Battersby *et al.* 2017; Padullés Cubino *et al.* 2018; Santacruz-García *et al.* 2019), quantitative estimation of trait-flammability relationships at the shoot-level is still in its infancy. Using ordinal trait values, Calitz *et al.* (2015) compared leaf size, leaf texture, leaf density and number of twigs, to shoot flammability, and showed that species with small leaves and more twigs had high flammability. Alam *et al.* (2019) found relationships between leaf functional traits and shoot flammability using species-level mean data on leaf morphological and chemical traits for 43 species, although they did not examine architectural traits. Alam *et al.* (2019) showed that a few key leaf traits (e.g. LDMC,

leaf lignin content) were highly correlated with shoot flammability, but some questions remain: will this relationship hold when the traits are measured in the same individual instead of being species-level averages gleaned from national databases, and when architectural traits are also considered? Furthermore, how well can we predict flammability from functional trait models?

In this study, we collected a range of leaf morphology and fuel architecture traits from 65 common indigenous and exotic New Zealand trees and shrubs and measured their flammability to: 1) examine the effect of leaf and architectural traits on shoot flammability; and 2) predict shoot flammability using functional traits. To our knowledge, this is the first shoot-level trait-flammability study to include quantitative measurements of leaf and architectural traits, and with all trait measurements made on the same individual plants on which flammability was measured.

3.3 Materials and methods

3.3.1 Sample collection

Plant samples were collected from 65 species of trees and shrubs from 42 families, commonly found in New Zealand forests, farms and gardens (Table S2.1). Among the species, 35 were indigenous to New Zealand, and the remaining 30 were exotic species that are commonly found there. These exotic species are commonly found in a range of habitat worldwide. The species were selected to represent a wide range of taxonomic groups. Samples were collected from: the arboretum and gardens of Lincoln University (most species); Hinewai Reserve, Bank Peninsula; a sheep and beef farm in North Canterbury; and a sheep and beef farm near Taumaranui, Waikato. Sampling and burning experiments were conducted during the spring and summer of 2018 and 2019. Samples were collected from six mature, healthy, and sun-exposed individuals of each species. From each plant, four leaves, three twigs and two, similar, 70-cm long terminal branches that best represented the average architecture of the whole canopy were collected (Jaureguiberry *et al.* 2011; Perez-Harguindeguy *et al.* 2013). For species that naturally retain dead material on their shoots (e.g. *Ulex europaeus*), such material was retained as part of the sample, as this has been shown to influence shoot flammability (Dent *et al.* 2019). Leaf and twig samples were immediately stored in zip-locked bags after collection to minimise the moisture loss of the freshly picked leaves (Perez-Harguindeguy *et al.* 2013). The branches were placed in sealed black plastic bags and stored in a fridge at 6-8°C before burning. The burning experiments were conducted within 48 hours of collection. The leaves, twigs and

one of the branches were used for measuring functional traits, while the other branch was used for flammability testing.

3.3.2 Functional trait measurements

Leaf-level traits

Functional traits of plants at leaf and shoot levels considered likely to be related to shoot flammability (Table S2.2) were measured using standard protocols (Perez-Harguindeguy *et al.* 2013). The leaves were immediately weighed to obtain fresh mass, and then leaf dimensions (length (cm), width (cm), thickness (mm)) were measured following Perez-Harguindeguy *et al.* (2013). Leaf area (cm^2) and perimeter (cm) were obtained from digital images through image processing software ImageJ 1.50i (National Institute of Health, USA). For leaves with a needle shape, leaf area was calculated as $2 \times length \times width$ and thickness by $diameter \times \pi/4$ (Pérez-Harguindeguy *et al.* 2013). The leaves were then weighed to obtain water-saturated mass after rehydration in water for 24 hours in the dark. The oven-dry mass was taken after drying the leaves in the oven at 65°C for 48 hours. Leaf volume (cm^3) was calculated by multiplying one-sided leaf area with thickness for broad leaves and by $\pi(\frac{diameter}{2})^2 * length$ for needle leaves (Grootemaat *et al.* 2015). The specific leaf area (SLA (cm^2/g)) and leaf surface area to volume ratio (SA:V (cm^{-1})) were estimated by dividing the leaf area by its oven-dry mass and leaf area by its volume respectively (Perez-Harguindeguy *et al.* 2013). Leaf moisture content (%), and leaf dry matter content (mg/g) were calculated following the equations:

$$\text{Leaf moisture content (LMC)} = \frac{Fresh\ leaf\ mass - Oven\ dry\ leaf\ mass}{Oven\ dry\ leaf\ mass} \times 100$$

$$\text{Leaf dry matter content (LDMC)} = \frac{Oven\ dry\ leaf\ mass}{Water\ saturated\ leaf\ mass}$$

Shoot-level architectural traits

Branching pattern

Branching pattern indicates the connectivity and continuity of fuel and was measured in each shoot as the: branching pattern on ramification point (BPRP) and branching pattern on stream order (BPSO). BPRP was measured by counting the number of live ramifications of a shoot

(Fig. S3.1a), and BPSO was measured by counting the number of sub-branches in a shoot following stream order (Fig. S3.1b) (Pérez-Harguindeguy *et al.* 2013).

Fuel volume

The volume of the shoot (cm^3) was calculated following the equation described by Thorne *et al.* (2002):

$$\text{Shoot Volume (SV)} = 2/3\pi H(\frac{A}{2} \times \frac{B}{2})$$

Where *H* is the length of the shoot, and *A* and *B* are the diameter taken at 50% of the shoot height with *B* perpendicular to *A*.

Fuel moisture content

To measure the moisture content of each shoot at the time of burning, a subsample of approximately 10 cm length, including both twigs and leaves was taken. The fresh mass of this subsample was measured at the time of burning and oven-dried for 48 hours at 65 ºC to obtain the dry mass. Fuel moisture content (FMC) on a dry mass basis of the sub-samples was then calculated as:

$$\text{FMC (\%)} = \frac{Fuel\ mass\ at\ burning - fuel\ dry\ mass}{Fuel\ dry\ mass} \times 100$$

Fuel density

Fuel bulk density (kg/cm^3) was measured by dividing shoot mass by its volume. Foliage fraction mass (FFM), and twig fraction mass (TFM) (g/cm^3) were measured by dividing the total mass of leaves, and twigs (< 5mm diameter) by the volume of the shoot. After calculating the volume of the shoot, all leaves and twigs were separated and weighed and then divided by the fuel volume of the shoot sample to obtain their density (Etlinger & Beall 2005).

Twig dry matter content

The twigs collected from the field were immediately rehydrated in water for 24 h and weighed for the water-saturated mass. They were then dried in the oven at 65°C for 48 h to obtain the oven-dry mass, and twig dry matter content (mg/g) was calculated following:

$$\text{Twig dry matter content (TDMC)} = \frac{Oven\ dry\ twig\ mass}{Water\ saturated\ twig\ mass}$$

3.3.3 Flammability measurements

The shoot samples were burnt and flammability measured using the device and methodology described by Jaureguiberry *et al.* (2011) and modified by Wyse *et al.* (2016) to meet New Zealand safety standards. The device consists of an 85 × 60 cm metal barrel cut in half longitudinally and placed horizontally on four metal legs of 100 cm length (Fig. S3.2). A burner was located 7 cm above the bottom of the barrel that remained on for the duration of the testing. A metal grill was positioned above the burners, and this was where the samples were placed for burning. A blowtorch (16.7 kW) located beneath the grill was used to ignite the sample. Both the burner and blowtorch were connected to an LPG cylinder (Fig. S3.2). Before burning, the shoot samples were air-dried for 24 hours to ensure the moisture content of the sample was suitable for the ignition source of the device, allowing comparison of flammability across species (Wyse *et al.* 2017).

To assess shoot flammability, first the burner was turned on, and the grill temperature was maintained c.150°C throughout the burning. Before placing the samples on the grill, the dimensions and weight of the shoot were measured. The samples were then placed horizontally on the grill to enable the maximum contact with the flames and pre-heated for 2 minutes to mimic an approaching fire where the adjacent plants are preheated by the radiant heat from the fire. The blowtorch was then turned on for 10 s, to provide a source of flaming ignition to the samples. Immediately after the blowtorch was turned off, the measurement of flammability variables commenced. Four flammability variables were recorded in this experiment: ignitibility was measured as time to ignition, the point at which the sample began to undergo flaming combustion independently of the blowtorch. Ignitibility ranged between 0 and 10 s and was rescaled inversely to derive an ignition score by giving higher values to those species that ignited quicker (e.g. an ignition time of 1 s was rescaled to a value of 9), and lower values to those species that took the longest to ignite (an ignition of 9 s was rescaled to 1). Samples that failed to ignite within 10 s were given a zero value. Combustibility was measured by recording the maximum temperature reached by the burning sample, and samples that failed to ignite were assigned a value of 150°C, representing the grill temperature. An infrared laser thermometer (Fluke 572; Fluke Corp., Everett, WA, USA) was used to record the maximum temperature of burning samples after the blowtorch was turned off by 'painting' the burning sample with the laser sights. Sustainability was measured as to how long the sample maintained flaming ignition after the blowtorch was turned off. Samples that did not burn without the blowtorch were assigned a burn time of zero. Consumability was recorded as a percentage of burnt biomass

after the flame was extinguished, calculated by visual observation by at least two observers. Samples that did not burn after the blowtorch was turned off were assigned zeros for consumability.

3.3.4 Data analysis

Analysis of variance (ANOVA) was used to determine whether plant functional traits and flammability variables differed significantly between species. To satisfy the assumptions of normality and homogeneity of variance, all parameters were log-transformed prior to ANOVA. The sum of squares data from the ANOVA was used to partition variance in each flammability variable into among-species and within-species components. The effects of functional traits on each of the flammability variables were assessed by a generalised linear model with a Gaussian family error distribution, and an identity link function for maximum temperature and a log link function for ignition score, burn time and burnt biomass, as determined by the distribution of the response variables in quantile-quantile plots. We visually verified the assumptions of normality and variance homogeneity of the residuals and tested the potential multicollinearity among explanatory variables of the models. Multicollinearity between the functional traits was assessed before variable inclusion in the models using Pearson's correlation coefficient and variance inflation factors (VIF) calculated using the function *vif* in the R package *car* (v 3.0-3) (John & Sanford 2011).

A correlogram plot (Fig. S3.3) showing the correlation matrix of all the functional traits was calculated using *corrgram* (v 1.13) package in R (Wright 2018). Due to strong correlations between some traits we restricted our analyses to nine, uncorrelated traits that maximised the trait variation analysed ($-0.6 < r < 0.6$; VIF < 2) (Zuur *et al.* 2010; Dormann *et al.* 2013). Correlation analysis indicated that leaf dimensional traits, including leaf length, leaf width, leaf perimeter, and leaf volume were highly correlated with leaf area, whereas LDMC was highly correlated with leaf moisture content (LMC), shoot moisture content (SMC) and twig dry matter content (TDMC). Leaf thickness was strongly correlated with leaf surface area to volume ratio (SAV). Therefore, leaf area, LDMC and leaf thickness were included in the final candidate models (Table 3.2). Among the correlated traits, we retained the one that had been more widely used in other studies as a predictor of flammability. All predictor variables were standardised using the *scale* function from *base* (v 3.6.1) package in R before analysis so that parameter estimates were on a comparable scale. Effect size plots visualizing the relationship between the

significant functional traits and each of the flammability variables were plotted using the function *effect_plot()* from the R-package *jtools* (v 2.0.1) (Long 2018).

To compare how well the different levels (leaf vs. architecture) of functional traits predict shoot-flammability, we first developed some plausible *a priori* candidate models for each flammability variable based on different combinations of leaf traits or architectural traits or both (Table 3.2). Among the leaf traits, we considered four traits, including leaf area (LA), leaf dry matter content (LDMC), specific leaf area (SLA), and leaf thickness (LT). Among the architectural traits, we considered five traits including branching pattern based on ramification point (BPRP), branching pattern based on stream order (BPSO), foliage fraction mass (FFM), twig fraction mass (TFM), and fuel bulk density (FBD) (Table 3.2).

Model performances were compared based on Akaike Information Criterion corrected for small sample size (AICc), AICc relative to the most parsimonious model (ΔAICc) calculated using *MuMin* (v 1.43.6) package in R (Barton 2019) and R^2 of the models calculated using the R-package *rsq* (v 1.1) (Zhang 2018). The best performing model for each flammability variable was then validated using *k*-fold cross-validation to assess how well it predicted the flammability of independent species (Kohavi 1995). Depending on the dataset, five fold cross-validation was performed by randomly dividing the data into five groups of even size and building five models in turn; each model using a different group as a test dataset, with the remaining four groups as the training dataset and repeating the process 100 times using the *caret* (6.0-84) package in R (Kuhn 2019). The overall model prediction error is the mean error from each of the individual cross-validations. The prediction accuracy between fitted and validated models was assessed based on the estimation of reduction of errors (Rebba *et al.* 2006) measured as root mean square error (RMSE) and mean absolute error (MAE). In addition, coefficient of determination (R^2) for both the fitted and validated models were compared for further assessment of the accuracy of the models. All analyses were performed using functions and routines implemented in the R software package version 3.6.1 (R Core Team, 2019).

3.4 Results

3.4.1 Variation in shoot flammability and functional traits among species

Flammability variables and functional traits varied across 65 species assessed (Table S3.3 & S3.4). The proportion of variance in all shoot flammability variables and functional traits was found to be higher among species (flammability variables: 77-94%; functional traits: 65-99%)

than within (flammability variables: 6-23%; functional traits: 1-35%) (Table S3.5). Species significantly varied in shoot-level flammability variables (ignition score: F_{64} = 79.17, P < 0.0001; maximum temperature: F_{64} = 17.24, P < 0.0001; burn time: F_{64} = 19.34, P < 0.0001; and burnt biomass: F_{64} = 42.38, P < 0.0001). The ignition score ranged from 0 (no ignition) to 9.5 (ignition within 0.5 s) with a mean across species of 5.3 ± 0.17 (ignition time of 4.7 s), while the maximum temperature was 788°C, with a species mean of 447.5 ± 9.15°C. The mean burn time across species was 15.7 ± 0.84 s and ranged from 0 to 85 s, and burnt biomass across species ranged from 0 to 95% with the mean across species of 28.9 ± 1.41 %. All the functional traits measured varied across the studied species; e.g. the leaf area of the species ranged from 0.03 to 169.06 cm^2 (Table S3.2).

3.4.2 Relationships between functional traits and shoot flammability

Leaf traits and fuel architectural traits were strongly related to the flammability variables. A substantial proportion of variation in ignitibility (R^2 = 0.54), combustibility (R^2 = 0.43), sustainability (R^2 = 0.41), and consumability (R^2 = 0.49) was explained by a combination of leaf functional traits and shoot-level architectural traits (Table 3.1). Of all the traits included in the model, LDMC was the most important for determining maximum temperature, burn time, and burnt biomass, whereas leaf thickness was the most important predictor trait for determining ignition score (Table 3.1). Among the leaf functional traits, LDMC, leaf thickness, and SLA were significant predictors of shoot flammability, whereas of the architectural traits branching pattern, foliage fraction mass, twig fraction mass, and fuel bulk density were significant predictors (Table 3.1). Both the LDMC and branching pattern showed a significant positive relationship with all flammability variables (Table 3.1) and species having high LDMC (Fig. 3.1 a, g & Fig. 3.2 a, e) and more sub-branches (Fig. 3.1 e, j & Fig. 3.2 c, g) ignited more quickly, burnt at a higher temperature, burnt longer and had greater biomass consumed. Leaf thickness was negatively associated with all flammability variables and with thick-leaved species having lower flammability, taking longer to ignite, burning more slowly at lower maximum temperatures and with less biomass consumed (Fig. 3.1 b, h & Fig. 3.2 b, f). In contrast, species with high SLA took longer to ignite (Fig. 3.1 c). Foliage fraction mass was significantly positively associated with burn time and negatively with burnt biomass, whereas twig fraction mass was significantly negatively associated with ignition score and maximum temperature (Table 3.1). Species with higher foliage fraction mass burnt for longer (Fig. 3.2 d), while higher twig mass per volume, reduced the ignitibility and combustibility (Fig. 3.1 f, k). Fuel bulk density significantly increased the maximum temperature (Table 3.1, Fig. 3.1 k).

Table 3.1 Contribution of leaf functional traits and fuel architectural traits to shoot-level flammability as determined by generalized linear models. Values represent coefficient estimates ± 1 SE of the slopes, and *P* values (‘***’$P < 0.001$, ‘**’$P < 0.01$, ‘*’ $P < 0.05$).

Traits	Ignition score	Maximum temperature (°C)	Burn time (s)	Burnt biomass (%)
Leaf area	0.048 ± 0.02	12.68 ± 8.79	0.017 ± 0.06	0.057 ± 0.04
Leaf dry matter content	0.180 ± 0.02 ***	98.49 ± 9.11 ***	0.475 ± 0.04 ***	0.426 ± 0.23 ***
Leaf thickness	-0.429 ± 0.04 ***	-40.54 ± 11.14 ***	-0.119 ± 0.05 *	-0.337 ± 0.06 **
Specific leaf area	-0.083± 0.03 **	-4.72 ± 11.01	-0.044± 0.06	0.012± 0.04
Branching pattern on ramification point	0.138 ± 0.02 **	32.58 ± 8.73 ***	0.062 ± 0.04	0.073± 0.04
Branching pattern on stream order	0.058 ± 0.02 *	37.57 ± 8.69 ***	0.129 ± 0.04 **	0.070 ± 0.02 *
Foliage fraction mass	-0.045 ± 0.03	10.19 ± 9.70	0.142 ± 0.03 ***	-0.142 ± 0.05 *
Twig fraction mass	-0.090 ± 0.02 **	-19.07 ± 8.38 *	-0.035 ± 0.03	0.064 ± 0.03
Fuel bulk density	-0.011 ± 0.02	23.717 ± 8.11 **	0.065 ± 0.04	0.060 ± 0.03
R^2	0.54	0.45	0.43	0.51

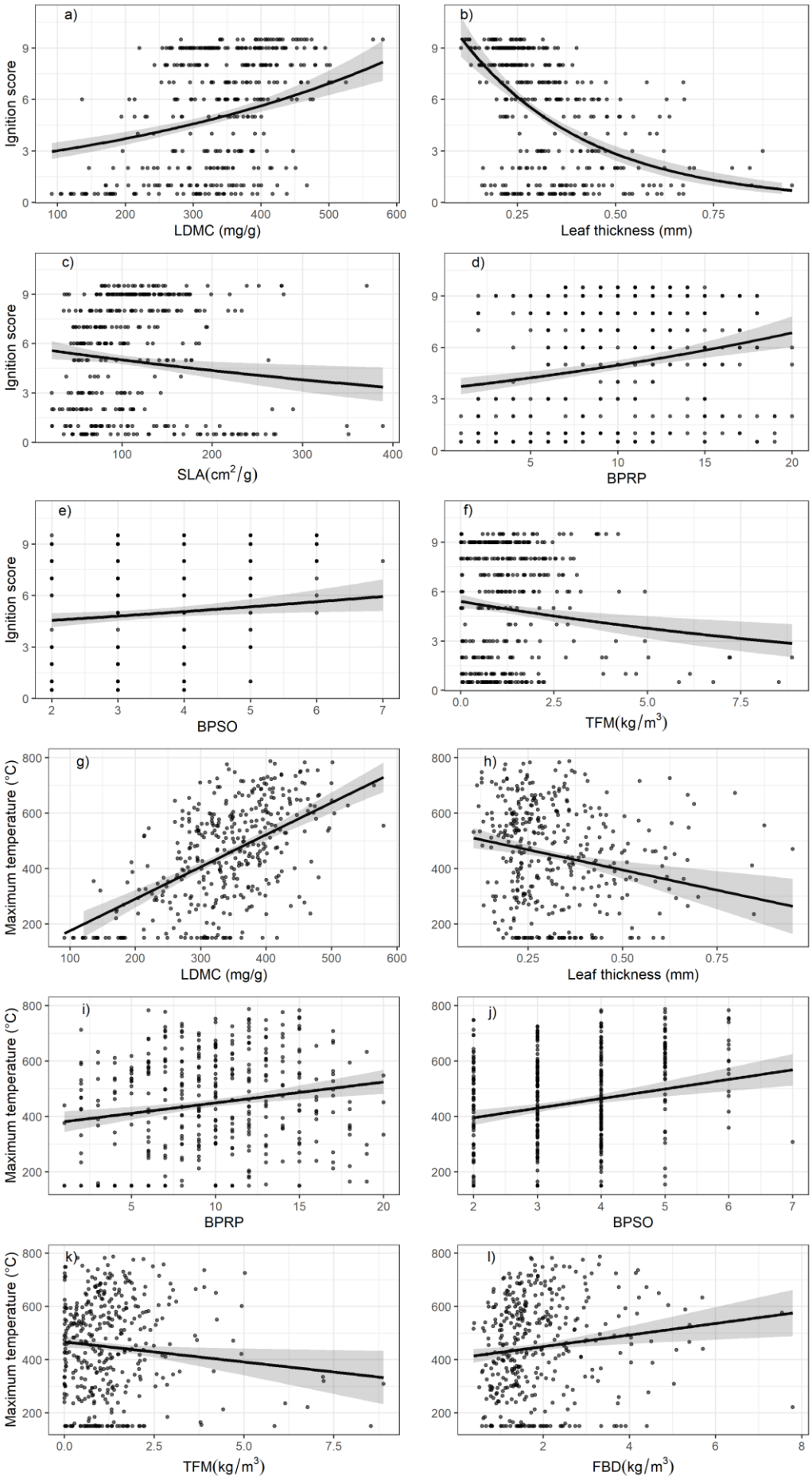
a)
Ignition score
LDMC (mg/g)
b)
Leaf thickness (mm)
c)
Ignition score
SLA(cm²/g)
d)
BPRP
e)
Ignition score
BPSO
f)
TFM(kg/m³)
g)
Maximum temperature (°C)
LDMC (mg/g)
h)
Leaf thickness (mm)
i)
Maximum temperature (°C)
BPRP
j)
BPSO
k)
Maximum temperature (°C)
TFM(kg/m³)
l)
FBD(kg/m³)

Figure 3.1 Plots showing the predicted (solid line) ignition score as a function of a) leaf dry matter content (LDMC), b) leaf thickness, c) specific leaf area (SLA), d) branching pattern based on ramification point (BPRP), e) branching pattern based on stream order (BPSO), f) twig fraction mass (TFM), and maximum temperature as a function g) leaf dry matter content (LDMC), h) leaf thickness, i) branching pattern based on ramification point (BPRP), j) branching pattern based on stream order (BPSO), k) twig fraction mass (TFM), l) fuel bulk density (FBD) from the generalised linear models. Black dots are the observed data points. The grey envelope represents the 95% confidence interval. The plots show the relationship between the flammability variables and each of the functional traits predicted by the model with all other variables held constant.

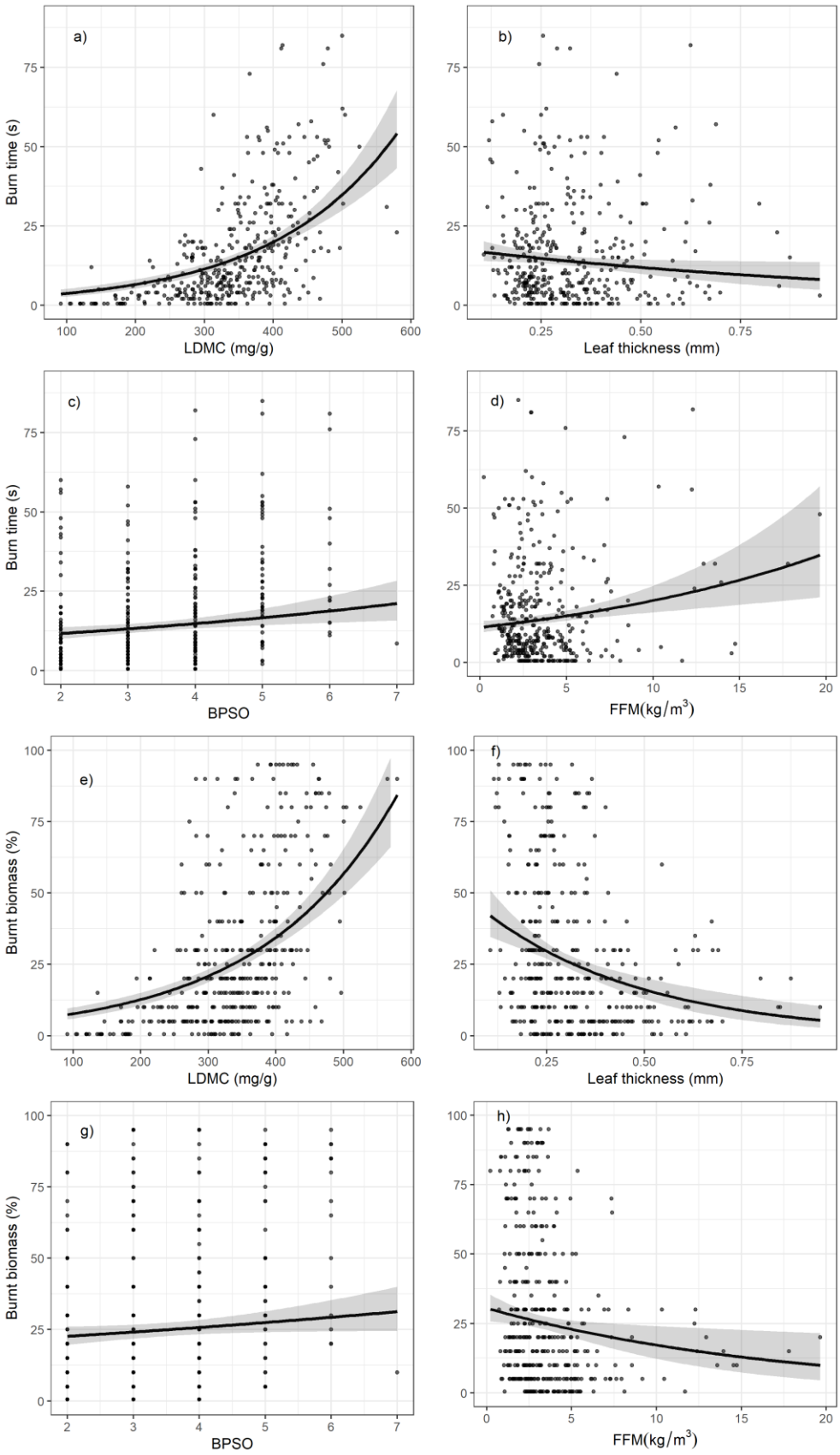
a)
b)
c)
d)
e)
f)
g)
h)
Burn time (s)
Burnt biomass (%)
LDMC (mg/g)
Leaf thickness (mm)
BPSO
FFM(kg/m3)

Figure 3.2 Plots showing the predicted (solid line) burn time as a function of a) leaf dry matter content (LDMC), b) leaf thickness, c) branching pattern based on stream order (BPSO), d) foliage fraction mass (FFM), and burnt biomass as a function of e) leaf dry matter content (LDMC), f) leaf thickness, g) branching pattern based on stream order (BPSO), h) foliage fraction mass (FFM) from the generalised linear models. Black dots are the observed data points. The grey envelope represents the 95% confidence interval. The plots show the relationship between the flammability variables and each of the functional traits predicted by the model with all other variables held constant.

3.4.3 Leaf and architectural traits predict shoot flammability

Shoot-level flammability measurements (ignition score, maximum temperature, burn time, and burnt biomass) were associated with leaf and fuel architectural traits. Among the plausible candidate models, the full model that included all the leaf and architectural traits performed best for predicting all four shoot flammability variables (highest R^2, lowest AICc, and AIC), ahead of the models that included only either leaf traits or structural traits or different combinations of leaf and architectural traits (Table 3.2).

Table 3.2 List of candidate models for evaluating the associated functional traits affecting the ignition score, maximum temperature, burn time and burnt biomass of plant at shoot-level, the results of model performance are based on corrected Akaike Information Criterion (AIC_c), AIC_c relative to the most parsimonious model (ΔAIC_c), and R^2 of the models. The most plausible models $\Delta AIC_c < 6$ for each flammability variable are in bold.

Candidate models	Model types	Ignition score			Maximum temperature			Burn time			Burnt biomass		
		AIC_c	ΔAIC_c	R^2	AIC_c	ΔAIC_c	R^2	AIC_c	ΔAIC_c	R^2	AIC_c	ΔAIC_c	R^2
LA+LT+SLA+LDMC+BPRP+ BPSO+FFM+TFM+FBD	Full model- all traits	**1767.16**	**0**	**0.54**	**4958.63**	**0**	**0.44**	**3104.66**	**0**	**0.41**	**3452.45**	**0**	**0.49**
LA+LT+SLA+LDMC	Leaf model	1801.34	34.17	0.49	4988.97	30.34	0.38	3138.19	33.54	0.35	3467.38	14.93	0.46
BPRP+BPSO+FFM+TFM+ FBD	Architecture model	1957.75	190.58	0.24	5111.43	152.81	0.15	3225.42	120.77	0.19	3637.52	185.07	0.17
LDMC+BPSO	Moisture & architecture	1961.96	194.8	0.22	4993.77	35.15	0.36	3120.03	15.37	0.37	3540.04	87.59	0.34
LA+LT+SLA+LDMC+FBD	Leaf traits and fuel load	1798.56	31.4	0.49	4986.61	27.98	0.38	3129	24.35	0.37	3467.44	14.99	0.46
LA+LT+LDMC	leaf size and moisture	1815.93	48.77	0.47	4987.23	28.6	0.38	3137.77	33.11	0.35	3468.68	16.23	0.46
LA+LT+SLA	Leaf size	1849.69	82.53	0.42	5105.79	147.16	0.16	3239.02	134.36	0.15	3581.75	129.3	0.27
LT+LDMC+BPSO+FFM+TFM	leaf, architecture and fuel mass	1798.61	31.44	0.49	4978.23	19.6	0.40	**3108.96**	**4.31**	**0.41**	**3454.76**	**2.31**	**0.48**
LT+LDMC+BPSO	Leaf size, moisture and architecture	1804.74	37.58	0.48	4978.48	19.85	0.39	3121.33	16.68	0.37	**3456.91**	**4.46**	**0.47**
LDMC+ BPSO+FFM+TFM	Moisture, architecture, fuel mass	1963.26	196.09	0.22	4984.48	25.86	0.38	3121.96	17.31	0.37	3541.59	89.14	0.35
LDMC+ BPSO+FFM+TFM +FBD	Moisture, architecture, fuel load	1909.72	142.56	0.32	4995.66	37.04	0.37	**3107.64**	**2.98**	**0.40**	3507.4	54.95	0.40

Candidate models	Model types	Ignition score			Maximum temperature			Burn time			Burnt biomass		
		AIC_c	ΔAIC_c	R^2	AIC_c	ΔAIC_c	R^2	AIC_c	ΔAIC_c	R^2	AIC_c	ΔAIC_c	R^2
LDMC+FFM+TFM	Moisture and fuel mass	1911.76	144.59	0.32	4988.86	30.23	0.38	**3106.49**	**1.84**	**0.40**	3502.81	50.35	0.41
LDMC+FBD	Moisture and bulk density	1913.59	146.42	0.31	5004.33	45.7	0.35	3121.99	17.34	0.37	3506.71	54.26	0.40
BPRP+BPSO+FFM+TFM	Branching pattern and fuel mass	1960.37	193.21	0.22	5003.27	44.64	0.35	3129.52	24.35	0.36	3553.33	100.88	0.32
FFM+TFM+FBD	Fuel mass and bulk density	1960.4	193.24	0.23	5128.56	169.93	0.11	3235.88	131.22	0.17	3647.76	195.31	0.15
LA	Single trait	2001.24	234.08	0.14	5160.98	202.35	0.03	3291.64	186.99	0.03	3670.05	217.6	0.09
LT	Single trait	2044.88	277.72	0.03	5164.82	206.2	0.01	3276.14	171.49	0.06	3689.49	237.04	0.03
SLA	Single trait	1930.75	163.58	0.27	5161.73	203.1	0.02	3300.16	195.51	0.00	3644.19	191.74	0.14
LDMC	Single trait	2055.49	288.33	0.00	5147.55	188.92	0.05	3269.07	164.42	0.08	3702.46	250.01	0.00
FBD	Single trait	1976.01	208.84	0.19	5003.11	44.48	0.34	3137.39	32.73	0.34	3551.57	99.12	0.32
BPRP	Single trait	2051.17	284.01	0.01	5162.43	203.8	0.01	3292.4	187.75	0.02	3702.36	249.91	0.00
BPSO	Single trait	2039.73	272.56	0.04	5158.26	199.63	0.02	3291.84	187.19	0.02	3697.34	244.89	0.01
FFM	Single trait	2016.49	249.33	0.10	5132.51	173.88	0.09	3246.29	141.64	0.13	3658.89	206.44	0.11
TFM	Single trait	2000.08	232.92	0.13	5167.03	208.4	0.00	3293.15	188.49	0.02	3673.11	220.65	0.07
FBD	Single trait	2054.26	287.1	0.00	5167.84	209.21	0.00	3296.32	191.67	0.01	3701.91	249.46	0.00
null model	null	2053.93	286.77	0.00	5165.93	207.3	0.00	3298.22	193.57	0.00	3700.73	248.28	0.00

The model that included all leaf and architectural traits performed well in predicting the flammability of independent species in the dataset. The cross-validation analysis showed that the models for ignition score, burn time and burnt biomass predicted independent data with higher accuracy than the fitted model, whereas the model for maximum temperature had lower predictive accuracy than the fitted model (Table 3.3). Across the four flammability models, the model for ignition score had the best performance in predicting values of the withheld species, with error reduced substantially compared to the fitted model (RMSE: 53% and MAE: 52%). The models for burn time and burnt biomass performed well (error reduced: RMSE, 38.9% and MAE, 31%; RMSE, 46% and MAE, 41% in validated model respectively), while the R^2 values were similar for the fitted and validated models for all four flammability variables (Table 3.3).

Table 3.3 Comparison of model performance (RMSE, MAE, and R^2) for predicting ignition score, maximum temperature, burn time and burnt biomass between the fitted model and the 5-fold cross-validated model.

Model	RMSE		MAE		R^2	
	Fitted	Validated	Fitted	Validated	Fitted	Validated
Ignition score	4.87	2.30 (1.97-2.67)	4.06	1.94 (1.66-2.23)	0.54	0.54 (0.42-0.66)
Maximum temperature	135.52	138.18 (120.64-163.55)	110.13	111.45 (97.40-128)	0.43	0.42 (0.22-0.59)
Burn time	20.84	12.73 (9.8-16.01)	13.53	9.29 (7.4-10.88)	0.41	0.41 (0.32-0.54)
Burnt biomass	37.49	19.94 (16.94-23.61)	26.21	15.43 (13.19-18.61)	0.49	0.49 (0.31-0.63)

Note: values in parenthesis show the ranges of the cross-validated models

3.5 Discussion

Plant flammability determines the burning behaviour of plants in wildfires and so linking plant functional traits to flammability is vital to allow upscaling to predict fire behaviour of vegetation from functional traits. Our primary aim of this study was to evaluate shoot-level trait-flammability relationships and whether shoot flammability variables can be predicted as a function of different leaf and fuel architectural traits. A criticism of laboratory-based flammability studies using small plant components such as a leaf or twigs is that they do not

represent the natural architecture of fuels. The complexity of burning whole plants makes it difficult to quantify the effect of plant architecture on flammability; however, burning a shoot preserves architecture (Jaureguiberry *et al.* 2011; Schwilk 2015), which enables assessment of the relative importance and the arrangement of fuel parts of crown fuels. It has been suggested that fire propagation from twig-to-twig on a shoot is likely to resemble the behaviour of fire as it moves from branch-to-branch in a canopy (Alam *et al.* 2019). Our study shows that a combination of certain leaf and fuel architectural traits can explain a substantial proportion of variation of four flammability variables measured at the shoot-level. Moreover, we identified the fuel architectural traits (branching pattern, foliage or twig fraction mass, and fuel bulk density) which are most related to shoot-flammability and hence likely to affect the burning behaviour of plants. This study also reveals that while certain functional traits are strongly related to shoot flammability, the latter is a complex plant character that requires data from a wide range of traits for appropriate prediction, including both easily-measured leaf traits and more complex and difficult-to-measure architectural traits.

3.5.1 Leaf traits such as LDMC, leaf thickness, and SLA influence shoot flammability

Leaf traits such as LDMC, leaf thickness, and SLA are critical determinants of plant flammability at the shoot-level. LDMC was the most crucial leaf trait, strongly positively correlated with all of the shoot flammability variables, showing that species with high leaf dry matter content are highly flammable. Species with high leaf dry matter content have low water content and higher dry mass per volume which makes them ignite more rapidly, burn for longer time at a higher intensity and causes more biomass to be consumed (Pompe & Vines 1966; Shipley & Vu 2002; Perez-Harguindeguy *et al.* 2013). This result is consistent with the findings of Alam *et al.* (2019) who showed that LDMC was the strongest predictor of flammability at the shoot-level when using species-level means gleaned from a national database for a range of leaf morphological and chemical traits. Alam *et al.* (2019) noted the need for confirmation of their findings by measuring traits and flammability on the same individuals, rather than relying on species means. Here we provide this confirmation, demonstrating the robustness of the LDMC-shoot flammability relationship. Moreover, both studies confirm the suggestion of Perez-Harguindeguy *et al.* (2013) in the standardised trait measurement handbook that LDMC is an important trait that is positively related to flammability, irrespective of whether LDMC and flammability are measured on the same individual plants or species means from databases are used.

LDMC was strongly correlated with other traits related to the water content of different plant components, such as leaf moisture content, shoot moisture content and twig dry matter content (Fig. S3.3), suggesting that a suite of traits related to fuel water content have a critical influence on flammability. Fuel moisture content is the trait related to flammability that is most widely used in modelling fire behaviour, with higher fuel moisture content causing a decrease in flammability (Pompe & Vines 1966; Rothermel 1972; Dimitrakopoulos & Papaioannou 2001; Chuvieco *et al.* 2009). While leaf moisture content varies widely with different factors (e.g. diurnal, seasonal) (Pellizzaro *et al.* 2007; Saura-Mas & Lloret 2007), leaf dry matter content of species varies less (Wilson *et al.* 1999), potentially making it a more suitable trait as a predictor of species flammability. Twig dry matter content was identified as another important trait positively correlated with plant flammability. Plants with high twig dry matter content dry out quickly, providing suitable fuel and helping to spread fire faster through the branches (Perez-Harguindeguy *et al.* 2013).

Leaf thickness was strongly negatively associated with all the shoot flammability variables, suggesting that thick-leaved plants are less flammable. This finding is consistent with other studies which found thicker leaves are hard to ignite and release less heat during burning, which contributes to reducing plants flammability (Montgomery & Cheo 1971; Grootemaat *et al.* 2015; Mason *et al.* 2016). Leaf thickness was negatively associated with ignitibility in another shoot flammability study (Alam *et al*. 2019; *Chapter 2*), but that relationship was mostly driven by a single thick-leaved species. Our study confirms that leaf thickness is another strong predictor of flammability at the shoot-level and that thick-leaved species take longer to ignite, burn slowly with lower heat release and lower biomass consumption.

SLA was significantly negatively associated with ignition score; species with high SLA took longer to ignite. A significant negative correlation between ignition score and SLA of species from tussock grasslands was found in another shoot-level study (Padullés Cubino *et al.* 2018). These consistent findings using plants of different growth forms suggest that SLA has some value in explaining the flammability of shoots. However, there was no relationship found between SLA and flammability in another shoot-level study that used species mean traits data (Alam *et al.* 2019). Furthermore, the negative relationship between SLA and shoot flammability is the converse of that found in leaf flammability studies, where high SLA is related to high ignitibility (Murray *et al.* 2013; Grootemaat *et al.* 2015). These contradictory findings for SLA can be explained by differences in leaf- and shoot-level flammability; Alam *et al.* (2019) found

no correlation between these different fuel levels suggesting that the mechanisms underpinning the burning of a single leaf and a shoot with multiples leaves and twigs are completely different.

3.5.2 Architectural traits such as branching pattern, leaf and twig fraction mass, and fuel bulk density influence shoot flammability

Fuel structure, arrangement, continuity and quantity influence flammability (Papió & Trabaud 1990; Martin *et al.* 1994; Zylstra *et al.* 2016) and our data showed that certain architectural traits at shoot-level, such as branching pattern (Fig. 3.3 a, b), foliage or twig fraction mass, and fuel bulk density strongly influence the flammability of a plant. Architectural traits, such as horizontal and vertical branching patterns indicate the continuity and spatial arrangement of fuels, which affects ignition, fire intensity, and spread rate (Miller & Urban 2000; Burger & Bond 2015; Pausas *et al.* 2017). Species with highly branched canopies (Fig. 3.3a) possess tightly spaced leaves and twigs, which promotes flammability by allowing efficient heat transfer (Saura-Mas *et al.* 2010; Schwilk 2015). Our findings suggest that shoots with many closely connected branches are highly flammable and ignite faster, burn for longer with high temperatures, consuming more fuel. This finding is consistent with the idea that fuel connectivity is vital to determining how fuel burns and fire spreads through the connected fuel (Cooper 1960; Dodge 1972; Calkin *et al.* 2014). Branching pattern is critical for crown fire, as vertical branches create ladder fuel that increases the probability of a surface fire propagating into the crown, while more lateral branches ensure connectivity of the aerial fuels, spreading the fire and causing intense canopy fires (Wagner 1977; Scott & Reinhardt 2001; Graham *et al.* 2004; Menning & Stephens 2007; Mitsopoulos & Dimitrakopoulos 2007).

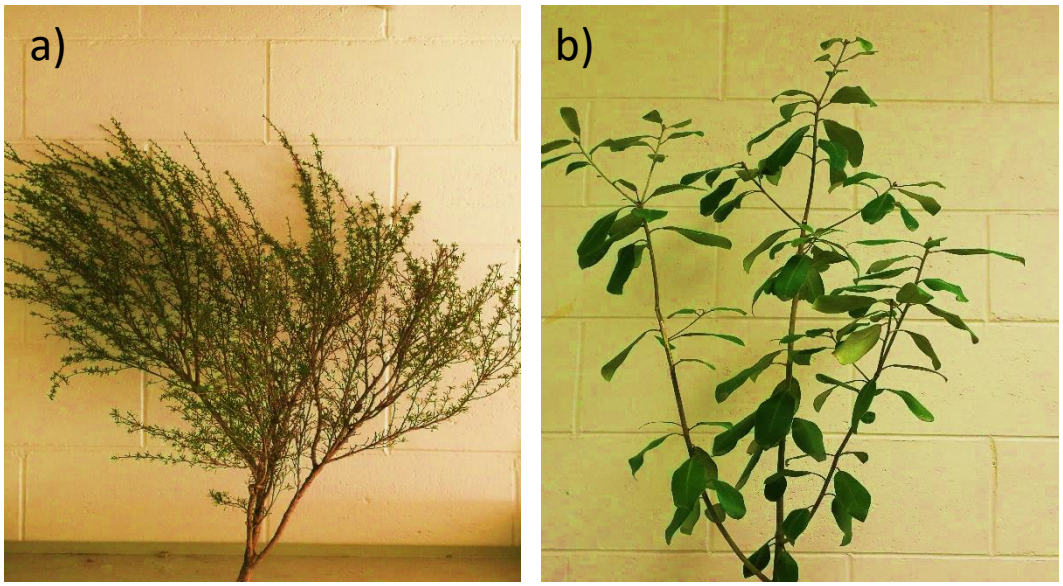

Figure 3.3 Photos of the branches from species a) with high branching pattern (image: *Kunzea robusta*) b) with low branching pattern (image: *Pittosporum ralphii*).

In our study, fuels with higher foliage fraction mass burned for a longer time, and high fuel bulk density significantly increased maximum temperatures of the fire. Live canopy foliage is the main fuel consumed during any crown fire and, along with crown fuel bulk density, it determines fuel load or availability (Alexander 1988; Wagner 1993). Our data indicate the importance of potential fuel availability in determining crown fire behaviour (Wagner 1977; Scott & Reinhardt 2001) and support Schwilk's (2015) contention that canopy fires are fuel limited. Higher foliage fraction mass results in more readily consumable fuel that continues to burn for longer; likewise, high bulk density means more biomass to consume that releases more heat (i.e. produces higher temperatures) during the burning. Canopy-level fuel bulk-density is one of the main factors of the crown fire model to assess crown fire potential, where high fuel bulk-density increases the spread and intensity of a crown fire (Wagner 1977, 1993; Mitsopoulos & Dimitrakopoulos 2007).

Identifying the leaf and architectural traits which best predict shoot flammability is useful for our mechanistic understanding of the combustion process in wildfires, and certain traits, such as LDMC, clearly make an important contribution to determining how well species burn. However, for many species, it is more efficient to simply measure their shoot flammability, rather than the range of traits needed to predict shoot flammability. Hence, we advocate ongoing research into the comparative shoot flammability of species from a wide range of biomes.

3.5.3 Modelling and predicting shoot flammability from functional traits

Flammability of plants is a complex characteristic, and predicting flammability is challenging due to its multifaceted nature and interaction with several physical and physiological factors (White & Zipperer 2010). Leaf physical, physiological, and fuel architectural traits all influence plant flammability and we attempted to make a predictive model from a range of leaf and architectural traits. Our study showed that a substantial proportion of variation of different flammability variables (ignitibility: 54%, combustibility: 45%, sustainability: 43% and consumability: 51%) was predicted using leaf morphological and fuel architectural traits, suggesting that plant traits are useful predictors of flammability. While many studies have identified trait-flammability relationships at different fuel levels, very few have attempted to produce predictive flammability models using functional traits. Grootemaat (2015) used leaf traits to predict the ignitibility of leaves and found that leaf thickness and SLA were the best predictors of leaf-level ignitibility. Also, a Forest Flammability Model was developed by Zylstra *et al.* (2016) to predict flame propagation through vegetation using leaf traits and vegetation structure.

Developing functional trait models to predict flammability is critical for choosing suitable species for vegetation management that can help to reduce damage from fires. Additionally, identification of the traits that predict flammability can be used in fire behaviour models to improve forecasts of wildfire behaviour. Both leaf and architectural traits influence flammability, and the full model including all the leaf and architectural traits was the best at predicting flammability. We did not identify any model that can usefully predict flammability using only a single trait, or models that include only a few traits that can be easily measured. This highlights the complex nature of plant flammability, demonstrating that it is driven by multiple traits. While we have shown that it is possible to estimate shoot flammability using a range of leaf and architectural traits, several of these traits, especially the architectural ones (such as branching pattern, foliage or twig fraction mass) can take a considerable time to measure (ca 30 min per samples).

Given that shoot flammability measurements take on average 5 min to complete, it might be more efficient to simply measure shoot flammability rather than the many functional traits needed to accurately assess species flammability. We also found that there was a large proportion of unexplained variation in the flammability models, suggesting that the inclusion of other traits such as leaf chemistry (e.g. volatile oils and resins, mineral content, and lignin)

might improve further model precision. Leaf volatile compounds are strongly related to flammability (Alessio *et al.* 2008; Chetehouna *et al.* 2009; Pausas *et al.* 2016), including shoot flammability (Alam *et al*. 2019), and could be included in fire behaviour models for better understanding of how plants burn. Furthermore, despite the potential of functional traits to predict flammability, they should be used in conjunction with environmental factors (i.e. temperature, wind, topography) to depict a complete scenario of fire behaviour of a given ecosystem.

3.5.4 Management implications

Understanding fire behaviour and managing vegetation to minimize fire hazard are one of the major challenges for scientists and fire managers. Changes in fire regimes in landscapes are influenced by the patterns of species composition, along with weather and topography (Beaty & Taylor 2001; Odion *et al.* 2010; Padullés Cubino *et al.* 2018). Efficient quantification of flammability will enhance our ability to manage vegetation in an era of extreme wildfires (Bowman *et al.* 2017). While the best way of quantifying vegetation flammability is via field-based experimental burns, this is not always feasible and is logistically complex to undertake. One alternative way to tackle this issue is to use functional traits to predict flammability. Our study shows that certain plant functional traits can be used to develop a predictive model to understand flammability. Many models have been developed to predict ecosystem fire behaviour (Rothermel 1972; Burgan & Rothermel 1984; Perry 1998; Scott & Reinhardt 2001), but most do not incorporate trait information related to flammability (Hall & Burke 2006; Zylstra *et al.* 2016). Future versions of these models should represent the influence of functional traits on flammability and fire behaviour.

While a suite of leaf and architectural traits predict species flammability, the traits representing moisture content of leaves (e.g. leaf moisture content, leaf dry matter content) or twigs (e.g. twig dry matter content; or stems, e.g. shoot moisture content) were most strongly associated with flammability variables. This outcome reinforces the importance of considering fuel moisture content in assessing wildland fire danger (Viegas *et al.* 1992; Chuvieco *et al.* 2004; Rossa 2017) and highlights that measuring the moisture content of plants at the landscape level could determine flammability and fire behaviour of vegetation. Fuel moisture content is a fundamental parameter in most models used to predict fire behaviour (Rothermel 1972; Malanson & Trabaud 1988; Scott & Burgan 2005). Our results further support global and national initiatives for fire hazard assessment by mapping fuel moisture content remotely

(Chuvieco *et al.* 2002; Danson & Bowyer 2004; Yebra *et al.* 2008; Myoung *et al.* 2018), and the development of global datasets of live fuel moisture content (e.g. Globe-LFMC; (Yebra *et al.* 2013, 2019)). The trait-flammability relationships identified in this study can also be included in dynamic global vegetation models. In particular, leaf traits (i.e., LDMC, leaf thickness) that are easy to measure, strongly linked to flammability and widely available in global trait databases (e.g. LDMC with 4941 species entries in the TRY trait database (Kattge *et al.* 2011) and 1735 species in the LEDA trait database (Kleyer *et al.* 2008)) can be useful to improve dynamic global vegetation models to understand global fire behaviour.

Another implication of our study is the demonstration of the importance of examining forest structure and composition when applying management treatments to vegetation in wildfire-prone regions. With increasing frequency of extreme wildfires in several parts of the world (Dennison *et al.* 2014; Balch *et al.* 2018; de la Barrera *et al.* 2018), effective fuel treatments can help to change the physical structure of the vegetation and reduce the likelihood of large intensive wildfires (Prichard *et al.* 2010; Cochrane *et al.* 2012; Stephens *et al.* 2012). Proper fuel modification can improve our ability to suppress wildfires quickly. Prescribed burning and mechanical thinning are the two common fuel treatments applied to forests (Graham *et al.* 1999; Schmidt *et al.* 2008). Prescribed burning is an efficient way to modify surface fuels and fires, whereas mechanical thinning helps to modify vegetation structure (Graham *et al.* 2004; Cochrane *et al.* 2012). Our study shows the way that architectural traits, such as fuel continuity between branches and fuel bulk density, change the flammability of a plant shoot, and further support the idea that fuel modification by mechanical treatment, such as reducing the continuity or connectivity of fuel, would help to reduce the spread of fire between branches of plants (Graham *et al.* 1999; Scott & Reinhardt 2001; Schmidt *et al.* 2008).

3.6 Conclusion

We identified strong relationships between functional traits and shoot-level flammability and demonstrated that a combination of leaf and architectural traits can be useful to predict the flammability of plants. While traits such as LDMC emerged as being important in explaining shoot flammability, the best models predicting flammability variables were ones that included the full range of leaf and architectural traits, highlighting the complex nature of flammability. Being a widely measured trait and readily available in global trait databases, LDMC shows great promise as a predictor of flammability and should be included in attempts to model fire behaviour. Likewise, remotely estimating and mapping fuel moisture content is another promising way of determining vegetation flammability and predicting fire behaviour. Plant architecture, such as branching pattern, strongly influence flammability and fire spread. These trait-flammability relationships highlight the potential of including these key functional traits in global fire behaviour models, potentially improving our prediction of fire behaviour and facilitating better fire and vegetation management in an increasingly fire-prone world. However, when trait data are lacking for a given species it may be most efficient and effective to simply measure shoot flammability.

3.7 Supplementary information

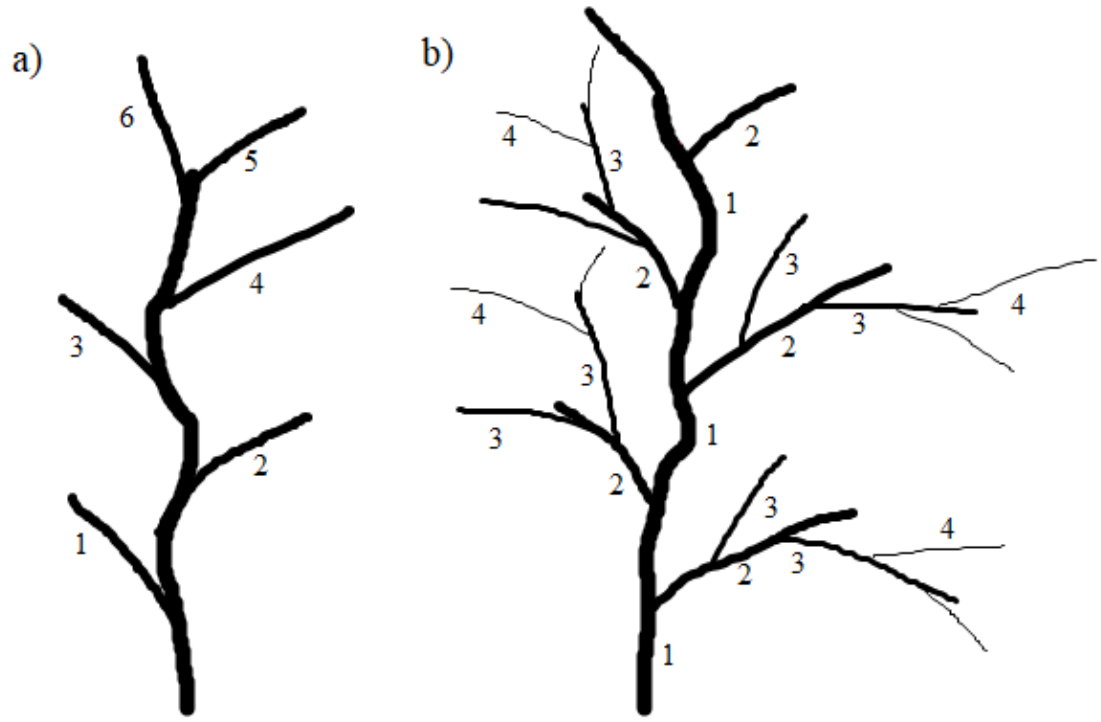

Figure S3.1 Schematic view of calculating branching pattern of the shoot samples a) branching pattern based on ramification point (BPRP) b) branching pattern based on stream order (BPSO).

Figure S3.2 The device used for burning shoot samples in this study

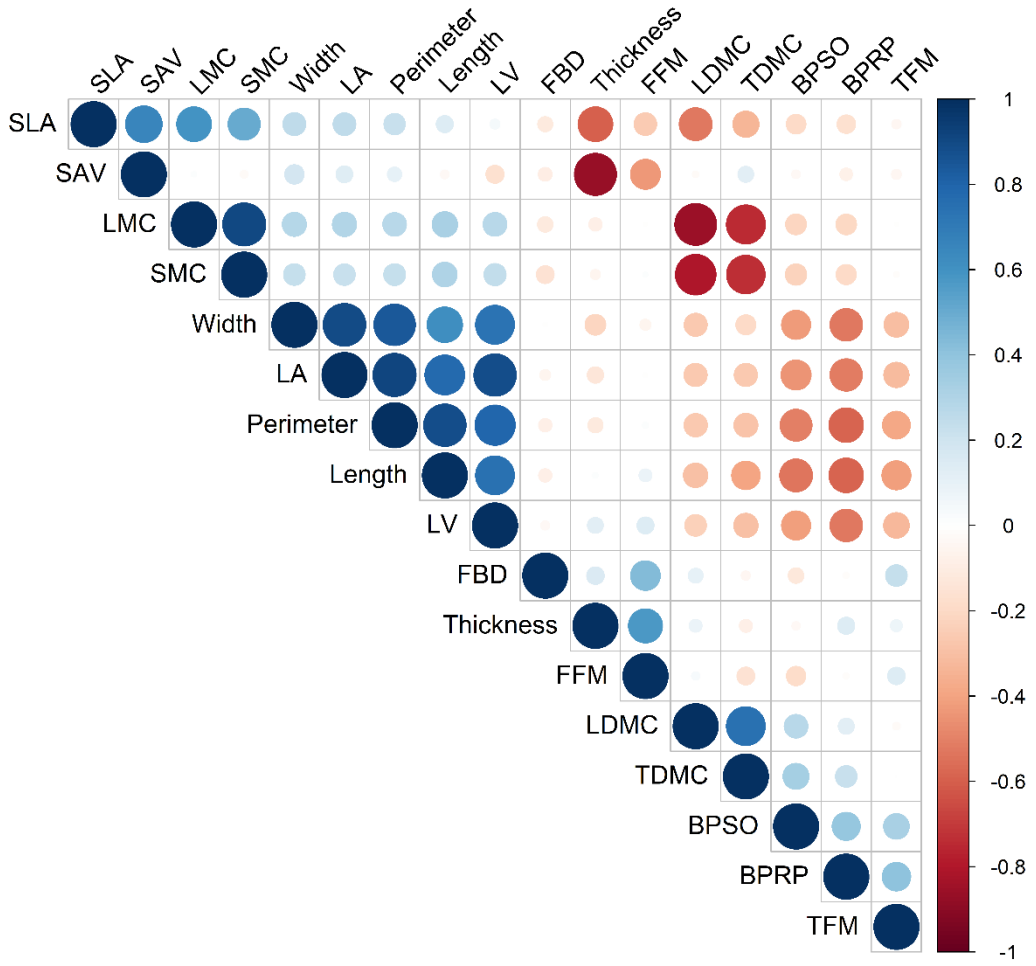

Figure S3.3 Correlogram showing the correlation coefficients between functional traits. Positive correlations are displayed in blue and negative correlations in red colour. Colour intensity and the size of the circle are proportional to the correlation coefficients. In the right side of the correlogram, the legend colour shows the correlation coefficients and the corresponding colours.

Table S3.1 Plant species included in this study, their code used for analysis, native ranges, structure and collection site. Taxonomy and indigenous range follow the Ngā Tipu Aotearoa – New Zealand Plants (see: https://www.landcareresearch.co.nz/resources/data/nzplants).

Species	Code	Family	Origin	Structure	Collection site
Silver wattle (*Acacia dealbata* Link.)	ACAdea	Fabaceae	Australia	Angiosperm trees	Lincoln university
Ovens wattle (*Acacia pravissima* F.Muell)	ACApra	Fabaceae	Australia	Angiosperm trees	Lincoln university
Horse chestnut (*Aesculus hippocastanum* L.)	AEShip	Hippocastanaceae	South East Europe	Angiosperm trees	Lincoln university
Kauri (*Agathis australis* (D.Don) Lindl. ex Loudon)	AGAaus	Araucariaceae	New Zealand	Gymnosperm tree	Lincoln university
Strawberry tree (*Arbutus unedo* L.)	ARBune	Ericaceae	Mediterranean, W. Europe	Angiosperm trees	Lincoln university
Wineberry (*Aristotelia serrata* J.R.Forst. & G.Forst.)	ARIser	Elaeocarpaceae	New Zealand	Angiosperm trees	Hinwai reserve
Silver birch (*Betula pendula* Roth.)	BETpen	Betulaceae	Europe and parts of Asia	Angiosperm trees	Lincoln university
Marble leaf (*Carpodetus serratus* J.R.Forst & G.Forst.)	CARser	Rousseaceae	New Zealand	Angiosperm trees	Hinwai reserve
Tree Lucerne (*Chamaecytisus palmensis* F.A.Bisby & K.W.Nicholls)	CHApal	Fabaceae	Canary Islands	Angiosperm trees	Lincoln university
Mexican orange (*Choisya ternate* Kunth.)	CHOter	Rutaceae	Mexico	Angiosperm trees	Lincoln university
Mingimingi (*Coprosma propinqua* A.Cunn)	COPpro	Rubiaceae	New Zealand	Angiosperm trees	Glenafric farm
Karamu (*Coprosma robusta* Raoul.)	COProb	Rubiaceae	New Zealand	Angiosperm trees	Lincoln university
Tutu (*Coriaria arborea* R.Linds.)	CORarb	Coriariaceae	New Zealand	Angiosperm trees	Glenafric farm
Scotch Broom (*Cytisus scoparius* L.)	CYTsco	Fabaceae	Western and central Europe	Angiosperm trees	Hinwai reserve
Kahikatea (*Dacrycarpus dacrydioides* (A.Rich.) de Laub.)	DACdac	Podocarpaceae	New Zealand	Gymnosperm Trees	Te Uranga farm
Akeake (*Dodonaea viscosa* Jacq.)	DODvis	Sapindaceae	New Zealand	Angiosperm trees	Lincoln university
Silver dollar gum (*Eucalyptus cinerea* F.Muell. ex Benth.)	EUCcin	Myrtaceae	Australia	Angiosperm trees	Lincoln university
Manna Gum (*Eucalyptus viminalis* Labill.)	EUCvim	Myrtaceae	Australia	Angiosperm trees	Lincoln university
European beech (*Fagus sylvatica* L.)	FAGsyl	Fagaceae	Southern England,	Angiosperm trees	Lincoln university

Green ash (*Fraxinus pennsylvanica* Marshall.)	FRApen	Oleaceae	Eastern and central North America	Angiosperm trees	Lincoln university
Tree fuchsia (*Fuchsia excorticata* (Forst. & Forst. f.) L. f.)	FUCexc	Onagraceae	New Zealand	Angiosperm trees	Hinwai reserve
Mountain Beech (*Fuscospora cliffortoides* (Hook.f.) Heenan and Smissen)	FUScli	Nothofagaceae	New Zealand	Angiosperm trees	Lincoln university
Red Beech (*Fuscospora fusca* (Hook.f.) Heenan and Smissen)	FUSfus	Nothofagaceae	New Zealand	Angiosperm trees	Lincoln university
Maidenhair tree (*Ginkgo biloba* L.)	GINbil	Ginkgoaceae	China	Gymnosperm Trees	Lincoln university
Broadleaf (*Griselinia littoralis* Raoul)	GRIlit	Cornaceae	New Zealand	Angiosperm trees	Hinwai reserve
Koromiko (*Hebe salicifolia* (G. Forst.) Pennell)	HEBsal	Plantaginaceae	New Zealand	Angiosperm trees	Lincoln university
Narrow-leaved Houhere (*Hoheria angustifolia* Raoul)	HOHang	Malvaceae	New Zealand	Angiosperm trees	Lincoln university
Kanuka (*Kunzea robusta* de Lange et Toelken)	KUNrob	Myrtaceae	New Zealand	Angiosperm trees	Hinwai reserve
Manuka (*Leptospermum scoparium* J.R.Forst. & G.Forst.)	LEPsco	Myrtaceae	New Zealand	Angiosperm trees	Glenafric farm
Himalayan honeysuckle (*Leycesteria Formosa* Wall.)	Leyfor	Caprifoliaceae	Himalaya and southwestern China	Angiosperm trees	Te Uranga farm
Broad-leaf privet (*Ligustrum lucidum* W.T.Aiton)	LIGluc	Oleaceae	China	Angiosperm trees	Lincoln university
Sweetgum (*Liquidambar styraciflua* L.)	LIQsty	Altingiaceae	Eastern North America	Angiosperm trees	Lincoln university
Southern magnolia (*Magnolia grandiflora* L.)	MAGgra	Magnoliaceae	Southeastern United States	Angiosperm trees	Lincoln university
Mayten tree (*Maytenus boaria* Molina.)	MAYboa	Celastraceae	South America	Angiosperm trees	Lincoln university
Mahoe (*Melicytus ramiflorus* J.R.Forst. and G.Forst.)	MELram	Violaceae	New Zealand	Angiosperm trees	Hinwai reserve
Ngaio (*Myoporum laetum* G.Forst.)	MYOlae	Scrophulariaceae	New Zealand	Angiosperm trees	Glenafric farm
Satinwood (*Nematolepis squamea* (Labill.) Paul G. Wilson)	NEMsqa	Rutaceae	Australia	Angiosperm trees	Lincoln university
Silver beech (*Lophozonia menziesii* (Hook.f.) Heenan et Smissen)	NOTmen	Nothofagaceae	New Zealand	Angiosperm trees	Lincoln university
Akiraho (*Olearia paniculata* (J.R.Forst. et G.Forst.) Druce)	OLEpan	Asteraceae	New Zealand	Angiosperm trees	Lincoln university

Chatham Island akeake (*Olearia traversiorum* (F.Muell.) Hook.f.)	OLEtra	Asteraceae	New Zealand	Angiosperm trees	Lincoln university
Kaikomako (*Pennantia corymbosa* J.R.Forst. et G.Forst.)	PENcor	Pennantiaceae	New Zealand	Angiosperm trees	Glenafric farm
Inkweed (*Phytolacca octandra* L.)	PHYoct	Phytolaccaceae	South & Central America	Angiosperm trees	Te Uranga farm
Radiata pine (*Pinus radiata* D.Don)	PINrad	Pinaceae	USA	Gymnosperm Trees	Lincoln university
Kawakawa (*Piper excelsum* G.Forst.)	PIPexc	Piperaceae	New Zealand	Angiosperm trees	Glenafric farm
Karo (*Pittosporum crassifolium* Banks and Sol. ex A.Cunn.)	PITcra	Pittosporaceae	New Zealand	Angiosperm trees	Lincoln university
Lemonwood (*Pittosporum eugenioides* A.Cunn)	PITeug	Pittosporaceae	New Zealand	Angiosperm trees	Hinwai reserve
Kohuhu (*Pittosporum tenuifolium* Sol. ex Gaertn)	PITten	Pittosporaceae	New Zealand	Angiosperm trees	Lincoln university
Ribbonwood (*Plagianthus regius* (Poit.) Hochr.)	PLAreg	Malvaceae	New Zealand	Angiosperm trees	Lincoln university
Mountain totara (*Podocarpus cunninghamii* Colenso)	PODcun	Podocarpaceae	New Zealand	Gymnosperm Trees	Hinwai reserve
Totara (*Podocarpus totara* G.Benn. ex D.Don)	PODtot	Podocarpaceae	New Zealand	Angiosperm trees	Te Uranga farm
Lombardy Poplar (*Populus nigra* L.)	POPnig	Salicaceae	Europe, southwest and central Asia, and northwest Africa	Angiosperm trees	Lincoln university
Western balsam-poplar (*Populus trichocarpa* Torr. & A.Gray ex. Hook.)	POPtri	Salicaceae	Western North America	Angiosperm trees	Lincoln university
Oleanderleaf protea (*Protea neriifolia* R.Br.)	PROner	Proteaceae	South Africa	Angiosperm trees	Lincoln university
Cherry laurel (*Prunus laurocerasus* L.)	PRUlau	Rosaceae	southwestern Asia and southeastern Europe	Angiosperm trees	Lincoln university
Japanese cherry (*Prunus serrulata* Lindl.)	PRUser	Rosaceae	China, Japan, and Korea	Angiosperm trees	Lincoln university
Matai (*Prumnopitys taxifolia* (D.Don) de Laub.)	PRUtax	Podocarpaceae	New Zealand	Gymnosperm Trees	Te Uranga farm
Five finger (*Pseudopanax arboreus* (L.f.) Allan)	PSEarb	Araliaceae	New Zealand	Angiosperm trees	Glenafric farm
Horopito (*Pseudowintera colorata* (Raoul) Dandy)	PSEcol	Winteraceae	New Zealand	Angiosperm trees	Hinwai reserve
Mountain five-finger (*Pseudopanax colensoi* (Hook.f.) Philipson var. colensoi)	PSEcole	Araliaceae	New Zealand	Angiosperm trees	Hinwai reserve

Lancewood (*Pseudopanax crassifolius* (Sol. ex A.Cunn.) C.Koch)	PSEcra	Araliaceae	New Zealand	Angiosperm trees	Hinwai reserve
Holm oak (*Quercus ilex* L.)	QUEile	Fagaceae	Mediterranean region	Angiosperm trees	Lincoln university
European oak (*Quercus robur* L.)	QUErob	Fagaceae	Europe	Angiosperm trees	Lincoln university
Chinese willow (*Salix matsudana* Koidz.)	SALmat	Salicaceae	Northeastern China	Angiosperm trees	Lincoln university
Poroporo (*Solanum laciniatum* Aiton)	SOLlac	Solanaceae	New Zealand	Angiosperm trees	Lincoln university
Laurustinus (*Vibranum tinus* L.)	VIBtin	Adoxaceae	Mediterranean area of Europe and North Africa	Angiosperm trees	Lincoln university

Table S3.2 Mean and range of the variables measured for flammability and functional traits, across the sixty-five species used in the study

Flammability variable	Mean	Range
Ignition score	5.34	0-9.5
Maximum temperature (°C)	447.46	150-638
Burn time (s)	15.74	0-85
Burnt biomass (%)	28.90	0-95
Functional trait		
Leaf length (cm)	7.69	0.4-27.75
Leaf width (cm)	3.45	3.45
Leaf thickness (mm)	0.32	0.32
Leaf area (cm^2)	22.55	22.55
Leaf perimeter (cm)	22.99	22.99
Leaf moisture content (%)	201.02	201.02
Leaf dry matter content (mg/g)	335.26	335.26
Twig dry matter content (mg/g)	370.84	370.84
Specific leaf area (cm^2/g)	112.6	112.6
Leaf volume (cm^3)	0.67	0.67
Surface area volume ratio (cm^{-1})	36.59	36.59
Branching pattern (ramification point)	9.7	1-20
Branching pattern (stream order)	3.536	2-25
Shoot moisture content (%)	185.36	38.81-710.32
Shoot volume (m^3)	0.031	0.004-0.149
Foliage fraction mass (kg/m^3)	3.58	0.217-31.44
Twig fraction mass (kg/m^3)	1.29	0.0043-8.88
Fuel bulk density (kg/m^3)	1.90	0.38-7.79

Table S3.3 Flammability variables values (mean ± 1 standard error) for the 65 species evaluated, and their influence on these variables. The final two rows indicate *F* values obtained from ANOVA and the degrees of freedom (*df*) for all flammability variables.

Species	Ignition score	Maximum temperature (°C)	Burn time (s)	Burnt biomass (%)
Acacia dealbata	9.5 ± 0	673.7 ± 32.7	41.67 ± 5.99	86.67 ± 2.47
Acacia pravissima	9.333 ± 0.105	594.8 ± 34.2	22.5 ± 0.885	65.83 ± 7
Aesculus hippocastanum	8.667 ± 0.211	456 ± 49.2	11 ± 1.88	20 ± 3.42
Agathis australis	1.167 ± 0.401	360.7 ± 58.4	12 ± 9.01	9.17 ± 4.17
Arbutus unedo	5.667 ± 0.955	648.8 ± 32.5	30 ± 5.39	43.33 ± 9.1
Aristotelia serrata	0.667 ± 0.333	226.8 ± 33.2	2.17 ± 1.08	4.17 ± 1.54
Betula pendula	9 ± 0	490 ± 37.7	16.33 ± 2.65	45.83 ± 5.83
Carpodetus serratus	8 ± 0	394.8 ± 58.4	5 ± 1.32	20 ± 4.28
Chamaecytisus palmensis	0.333 ± 0.211	163 ± 10.3	0.667 ± 0.422	1.67 ± 1.05
Choisya ternata	6.5 ± 0.224	446.5 ± 30.7	5.667 ± 0.989	15.83 ± 1.54
Coprosma propinqua	2 ± 0.516	265.2 ± 49.7	4.83 ± 1.85	8.33 ± 2.79
Coprosma robusta	5.667 ± 0.558	570.3 ± 44.8	10.33 ± 4.78	28.33 ± 8.72
Coriaria arborea	9 ± 0	654.3 ± 24.8	18.17 ± 3.96	53.33 ± 8.03
Cytisus scoparius	2.167 ± 0.833	292.2 ± 24.6	7.83 ± 1.54	8.33 ± 1.67
Dacrycarpus dacrydioides	9 ± 0	573.7 ± 52.8	25.5 ± 6.93	46.67 ± 6.67
Dodonaea viscosa	8.667 ± 0.211	468.7 ± 71.2	12.95 ± 2.45	27.5 ± 8.83
Eucalyptus cinerea	6.5 ± 0.224	646.3 ± 45.9	29.17 ± 5.35	55 ± 7.3
Eucalyptus viminalis	8.5 ± 0.224	702 ± 27.9	40.1 ± 4.61	79.17 ± 5.97
Fagus sylvatica	8.333 ± 0.211	553.5 ± 20.6	21.67 ± 3.43	65 ± 3.65
Fraxinus pennsylvanica	8.167 ± 0.307	554.3 ± 38.9	28.33 ± 8.17	47.5 ± 11.4
Fuchsia excorticata	0.167 ± 0.167	166.8 ± 16.8	0.333 ± 0.333	0.833 ± 0.833
Ginkgo biloba	1.833 ± 0.477	448.8 ± 25.6	5.83 ± 1.38	9.17 ± 2.01
Griselinia littoralis	0.833 ± 0.167	351.3 ± 30.3	5.83 ± 1.05	5 ± 0
Hebe salicifolia	2.5 ± 0.224	267.8 ± 32.3	2.833 ± 0.307	5 ± 0
Hoheria angustifolia	9 ± 0	382.7 ± 59.2	7.33 ± 1.41	30.83 ± 4.17
Kunzea robusta	9.5 ± 0	674.3 ± 36.5	20.17 ± 1.4	89.167 ± 0.833
Leptospermum scoparium	9.5 ± 0	617.2 ± 44.4	43.33 ± 4.07	92.5 ± 1.71
Leycesteria formosa	8.5 ± 0.224	513.5 ± 68.9	17.67 ± 5.95	59.17 ± 8.6
Ligustrum lucidum	1.833 ± 0.307	410 ± 38.4	17.17 ± 4.5	5 ± 0
Liquidambar styraciflua	9 ± 0	557.8 ± 10.1	6.5 ± 0.922	27.5 ± 3.1
Magnolia grandiflora	2.667 ± 0.211	476 ± 45.2	24.5 ± 4.98	12.5 ± 1.12
Maytenus boaria	9 ± 0	399.7 ± 26.4	7.333 ± 0.558	26.67 ± 2.79
Melicytus ramiflorus	5.5 ± 0.224	413.3 ± 50	5.5 ± 0.847	14.17 ± 2.01
Myoporum laetum	2.833 ± 0.601	336.7 ± 32.4	3.5 ± 0.619	10 ± 2.24
Nematolepis squamea	6.833 ± 0.167	358.5 ± 28.2	11.83 ± 2.68	18.33 ± 2.11
Nothoagus fusca	8 ± 0.258	550.7 ± 38	17.33 ± 1.89	28.33 ± 2.11
Nothofagus cliffortioide	8.5 ± 0.224	722.8 ± 21.5	53.67 ± 9.49	58.33 ± 5.87
Nothofagus menziesii	6.667 ± 0.211	626.7 ± 18.8	64 ± 5.69	75.83 ± 2.01

Olearia paniculata	6 ± 0.258	545.8 ± 40.4	33.8 ± 10	27.5 ± 5.12
Olearia traversiorum	5.5 ± 0.224	409 ± 36.1	17.67 ± 1.05	15 ± 5.16
Pennantia corymbosa	3.5 ± 0.847	403.2 ± 48.9	7.17 ± 2.55	10.83 ± 2.39
Phytolacca octandra	0 ± 0	150 ± 0	0 ± 0	0 ± 0
Pinus radiata	4.5 ± 0.342	436 ± 22.1	16 ± 3.01	24.17 ± 2.39
Piper excelsum	0 ± 0	150 ± 0	0 ± 0	0 ± 0
Pittosporum crassifolium	1.167 ± 0.401	397.3 ± 36.5	8.33 ± 3.62	5 ± 0
Pittosporum eugenioides	5.667 ± 0.333	414.5 ± 56.8	6.83 ± 1.01	14.17 ± 2.01
Pittosporum tenuifolium	8.667 ± 0.211	351.2 ± 20.7	5.5 ± 0.719	21.67 ± 2.47
Plagianthus regius	8.333 ± 0.333	403 ± 39.1	6.5 ± 1.93	19.17 ± 3.75
Podocarpus cunninghamii	1.833 ± 0.307	512 ± 73.5	26.8 ± 11.9	16.67 ± 3.33
Podocarpus totara	6 ± 0.365	567.8 ± 43.5	30 ± 5.77	37.5 ± 4.79
Populus nigra	9 ± 0	583.8 ± 45.6	11.9 ± 1.95	48.33 ± 4.77
Populus trichocarpa	0.833 ± 0.307	334.2 ± 70	4.5 ± 1.91	5.83 ± 2.39
Protea neriifolia	2.667 ± 0.333	510.8 ± 22.7	36.33 ± 5.23	16.67 ± 2.11
Prumnopitys taxifolia	5.667 ± 0.667	382.7 ± 48.4	11.33 ± 2.14	16.67 ± 2.47
Prunus kanzan	8 ± 0	701.5 ± 18.8	29.17 ± 3.22	67.5 ± 3.1
Prunus laurocerasus	0.5 ± 0.224	232.3 ± 41.6	3.67 ± 1.84	3.33 ± 1.05
Pseudopanax arboreus	0.333 ± 0.211	196.2 ± 30.4	3.5 ± 2.08	2.5 ± 1.12
Pseudopanax colensoi	0.833 ± 0.307	255.7 ± 52.3	2.33 ± 1.05	2.5 ± 1.12
Pseudopanax crassifolius	0 ± 0	186.8 ± 36.8	1.5 ± 1.5	0.833 ± 0.833
Pseudowintera colorata	6.167 ± 0.307	607.7 ± 16.1	36.33 ± 4.71	47.5 ± 6.55
Quercus ilex	8 ± 0.365	460.3 ± 58.9	23.93 ± 6.05	26.67 ± 7.92
Quersus robur	9.5 ± 0	678 ± 17.8	14.67 ± 1.61	95 ± 0
Salix matsudana	8.833 ± 0.167	428.8 ± 37.1	7 ± 1.77	23.33 ± 4.22
Solanum laciniatum	0 ± 0	150 ± 0	0 ± 0	0 ± 0
Vibranum tinus	6.667 ± 0.333	626.2 ± 10.1	18 ± 4.84	30 ± 3.65
F-Value	79.17***	17.24***	19.34***	42.38***
df	64	64	64	64

*** Statistical significance ($P < 0.001$).

Table S3.4 The influence of species on plant trait values (mean ± standard error) of 65 species as indicated by *F* values obtained from ANOVA. ***, *P* < 0.001.

Species	Length (cm)	Width (cm)	Thickness (mm)	Leaf area (cm^2)	Perimeter (cm)	LMC (%)
Acacia dealbata	0.5292 ± 0.0136	0.05833 ± 0.00132	0.12313 ± 0.00218	0.03938 ± 0.00106	1.2527 ± 0.0237	98.3 ± 10.1
Acacia pravissima	1.225 ± 0.0668	1.233 ± 0.311	0.25167 ± 0.00573	0.8794 ± 0.0625	4.1 ± 0.147	128.13 ± 5.42
Aesculus hippocastanum	20.68 ± 1.53	9.037 ± 0.583	0.13375 ± 0.00727	103.1 ± 14.2	64.91 ± 7.86	187.32 ± 8.2
Agathis australis	8.56 ± 2.71	1.3042 ± 0.0932	0.6403 ± 0.0281	6.029 ± 0.682	14.385 ± 0.839	122.18 ± 9.91
Arbutus unedo	7.625 ± 0.338	2.858 ± 0.159	0.33236 ± 0.00825	10.84 ± 1.02	17.02 ± 0.9	135 ± 5.8
Aristotelia serrata	8.208 ± 0.244	5.862 ± 0.281	0.17542 ± 0.0075	33.22 ± 2.87	35.05 ± 2.14	359.9 ± 24.7
Betula pendula	5.2 ± 0.268	4.379 ± 0.289	0.2225 ± 0.00612	14.05 ± 1.78	22.5 ± 1.46	148.83 ± 4.12
Carpodetus serratus	6.754 ± 0.272	3.45 ± 0.147	0.17292 ± 0.00538	14.23 ± 1.05	19.395 ± 0.8	218.18 ± 9.34
Chamaecytisus palmensis	3.713 ± 0.163	1.2458 ± 0.0751	0.2646 ± 0.0288	2.955 ± 0.169	8.341 ± 0.27	250.9 ± 12.4
Choisya ternata	7.087 ± 0.2	2.825 ± 0.101	0.33042 ± 0.0097	13.239 ± 0.894	18.418 ± 0.414	184.2 ± 10.3
Coprosma propinqua	1.025 ± 0.0183	0.504 ± 0.145	0.3175 ± 0.00483	0.176 ± 0.0164	2.1909 ± 0.0592	194.6 ± 10.5
Coprosma robusta	8.412 ± 0.381	4.125 ± 0.197	0.3579 ± 0.0183	24.21 ± 2	23.953 ± 0.831	198.1 ± 12
Coriaria arborea	7.417 ± 0.226	3.475 ± 0.0933	0.3 ± 0.012	21.68 ± 1.5	19.938 ± 0.655	197.46 ± 2.76
Cytisus scoparius	1.4375 ± 0.0412	0.475 ± 0.0204	0.22542 ± 0.00765	0.508 ± 0.0296	3.558 ± 0.107	243.1 ± 28.9
Dacrycarpus dacrydioides	0.5458 ± 0.0373	0.0991 ± 0.000833	0.2025 ± 0.00834	0.04562 ± 0.00368	1.59 ± 0.0861	113.56 ± 6.38
Dodonaea viscosa	9.483 ± 0.276	2.1875 ± 0.0543	0.25172 ± 0.0083	10.604 ± 0.569	18.503 ± 0.669	189.9 ± 12.5
Eucalyptus cinerea	6.25 ± 0.24	3.587 ± 0.138	0.34333 ± 0.00373	13.12 ± 1.23	15.96 ± 1.06	118.1 ± 2.61
Eucalyptus viminalis	13.379 ± 0.792	1.954 ± 0.112	0.3554 ± 0.0109	13.17 ± 1.08	31.2 ± 1.86	114.29 ± 2.77
Fagus sylvatica	7.913 ± 0.228	5.163 ± 0.12	0.15188 ± 0.00221	28.6 ± 1.69	26.32 ± 1.19	129.05 ± 2.03
Fraxinus pennsylvanica	10.942 ± 0.684	3.908 ± 0.209	0.1898 ± 0.0103	27.41 ± 3.16	28.9 ± 2.06	192.5 ± 13.8
Fuchsia excorticata	7.513 ± 0.282	2.804 ± 0.189	0.3215 ± 0.0133	13.67 ± 1.15	18.904 ± 0.577	475.5 ± 44.3
Ginkgo biloba	4.617 ± 0.176	6.738 ± 0.158	0.3492 ± 0.0167	19.24 ± 1.1	24.51 ± 1.75	157.24 ± 8.13
Griselinia littoralis	10.133 ± 0.368	5.45 ± 0.195	0.4573 ± 0.0288	42.52 ± 2.56	31.69 ± 1.03	261.8 ± 13
Hebe salicifolia	8.2 ± 0.441	2.217 ± 0.104	0.28208 ± 0.00827	11.09 ± 1.04	17.827 ± 0.977	247.2 ± 10.4
Hoheria angustifolia	3.825 ± 0.177	1.0667 ± 0.0519	0.2475 ± 0.0166	2.855 ± 0.236	10.97 ± 0.526	226.4 ± 12.5

Kunzea robusta	1.0708 ± 0.0362	0.12917 ± 0.00768	0.18958 ± 0.00119	0.15163 ± 0.00893	2.563 ± 0.153	138.09 ± 7.52
Leptospermum scoparium	0.75 ± 0.025	0.3333 ± 0.0124	0.2575 ± 0.0123	0.15275 ± 0.00539	1.9349 ± 0.0476	104.43 ± 7.8
Leycesteria formosa	12.983 ± 0.968	8.829 ± 0.825	0.2518 ± 0.0104	79.6 ± 13.6	44.31 ± 3.67	243.41 ± 8.04
Ligustrum lucidum	10.067 ± 0.422	5.321 ± 0.262	0.4421 ± 0.0181	33.57 ± 2.45	31.93 ± 2.17	193.6 ± 6.69
Liquidambar styraciflua	14.529 ± 0.371	18.092 ± 0.586	0.21312 ± 0.00182	127.16 ± 7.17	87.03 ± 2.93	201.35 ± 2.49
Magnolia grandiflora	17.254 ± 0.838	7.95 ± 0.331	0.4467 ± 0.015	96.79 ± 6.53	53.46 ± 1.96	145.74 ± 3.45
Maytenus boaria	2.563 ± 0.122	0.7917 ± 0.0587	0.22458 ± 0.00575	1.603 ± 0.154	6.962 ± 0.288	205.89 ± 8.33
Melicytus ramiflorus	11.721 ± 0.532	3.971 ± 0.357	0.21354 ± 0.00411	34.4 ± 4.58	33.23 ± 1.54	327.4 ± 21.5
Myoporum laetum	7.683 ± 0.233	2.4 ± 0.245	0.4906 ± 0.0283	14.81 ± 1.85	21.175 ± 0.663	362.6 ± 11.5
Nematolepis squamea	5.863 ± 0.19	1.3375 ± 0.0212	0.34083 ± 0.00756	5.855 ± 0.273	14.435 ± 0.456	149 ± 5.11
Nothoagus fusca	3.329 ± 0.144	2.288 ± 0.122	0.21472 ± 0.00983	5.56 ± 0.595	11.498 ± 0.585	145.34 ± 5.95
Nothofagus cliffortioide	1.3792 ± 0.0534	0.7792 ± 0.0454	0.2779 ± 0.0162	0.8696 ± 0.06	4.085 ± 0.159	106.5 ± 9.53
Nothofagus menziesii	1.2417 ± 0.0247	0.9625 ± 0.00854	0.255 ± 0.00266	1.0025 ± 0.0301	4.6986 ± 0.0721	96.58 ± 4.06
Olearia paniculata	5.638 ± 0.176	3.092 ± 0.112	0.3876 ± 0.0221	12.389 ± 0.4	19.29 ± 0.398	157.72 ± 8.85
Olearia traversiorum	4.208 ± 0.263	1.775 ± 0.133	0.5019 ± 0.0248	5.342 ± 0.745	11.35 ± 0.765	182.95 ± 9.62
Pennantia corymbosa	5.6292 ± 0.0734	3.329 ± 0.19	0.2917 ± 0.0123	13.485 ± 0.864	17.11 ± 0.542	243.06 ± 9.47
Phytolacca octandra	15.5 ± 0.83	6.217 ± 0.473	0.3487 ± 0.0112	67.66 ± 9.45	43.69 ± 3.09	758.7 ± 35.9
Pinus radiata	10.779 ± 0.138	0.05408 ± 0.00101	0.42477 ± 0.00793	11.645 ± 0.23	20.775 ± 0.438	148.33 ± 2.39
Piper excelsum	10.908 ± 0.217	10.854 ± 0.292	0.22854 ± 0.00361	58.65 ± 3.03	34.684 ± 0.842	585.16 ± 5.28
Pittosporum crassifolium	5.55 ± 0.189	2.3 ± 0.147	0.6096 ± 0.0201	8.773 ± 0.773	15.511 ± 0.519	142.71 ± 6.18
Pittosporum eugenioides	12.2 ± 0.363	3.3792 ± 0.0644	0.23042 ± 0.00735	32.59 ± 1.41	46.39 ± 3.52	180.88 ± 6.61
Pittosporum tenuifolium	5.204 ± 0.383	2.492 ± 0.144	0.2601 ± 0.0146	9.85 ± 1.19	14.758 ± 0.92	140.16 ± 5.47
Plagianthus regius	3.958 ± 0.179	1.974 ± 0.196	0.21937 ± 0.00957	4.762 ± 0.516	13.32 ± 1.06	212.5 ± 8.73
Podocarpus cunninghamii	1.3458 ± 0.0472	0.3542 ± 0.01	0.8229 ± 0.0446	0.3398 ± 0.0235	3.197 ± 0.161	138.08 ± 4.5
Podocarpus totara	2.071 ± 0.103	0.3 ± 0.00645	0.6233 ± 0.0211	0.5501 ± 0.0273	4.772 ± 0.215	140.17 ± 2.14
Populus nigra	7.633 ± 0.196	6.921 ± 0.243	0.2253 ± 0.0115	22.204 ± 0.748	24.95 ± 1.3	205.1 ± 7.13
Populus trichocarpa	12.938 ± 0.61	8.088 ± 0.355	0.2673 ± 0.0142	61.57 ± 5.05	36.97 ± 1.9	173.96 ± 9.82
Protea neriifolia	14.417 ± 0.59	2.671 ± 0.177	0.5304 ± 0.0166	28.33 ± 2.27	38.45 ± 2.19	159.27 ± 7.54
Prumnopitys taxifolia	1.5833 ± 0.0664	0.1833 ± 0.0124	0.4708 ± 0.0179	0.2849 ± 0.016	3.7087 ± 0.0903	140.34 ± 8.97
Prunus kanzan	11.179 ± 0.429	5.642 ± 0.158	0.22875 ± 0.00396	42.17 ± 2.74	45.63 ± 1.66	137.69 ± 4.63

Prunus laurocerasus	14.338 ± 0.492	5.304 ± 0.242	0.36264 ± 0.007	51.77 ± 3.84	36.282 ± 0.968	163.9 ± 2.93
Pseudopanax arboreus	10.217 ± 0.62	4.587 ± 0.419	0.43125 ± 0.00681	35.45 ± 5.85	32.48 ± 2.8	189.51 ± 5.03
Pseudopanax colensoi	12.875 ± 0.241	4.0167 ± 0.0546	0.3767 ± 0.0108	29.25 ± 1.14	33.23 ± 1.15	230.51 ± 8.21
Pseudopanax crassifolius	15.392 ± 0.178	1.925 ± 0.0793	0.5654 ± 0.0172	20.544 ± 0.548	36.023 ± 0.672	202.87 ± 3.86
Pseudowintera colorata	5.142 ± 0.219	2.475 ± 0.088	0.294 ± 0.0107	9.567 ± 0.742	14.682 ± 0.605	175.75 ± 4.82
Quercus ilex	7.029 ± 0.147	2.163 ± 0.118	0.27569 ± 0.00353	9.711 ± 0.892	16.839 ± 0.759	94.71 ± 5.86
Quersus robur	10.425 ± 0.2	7.238 ± 0.293	0.18687 ± 0.00618	41.63 ± 1.98	43.53 ± 2.7	122.41 ± 7.39
Salix matsudana	9.279 ± 0.29	1.375 ± 0.0629	0.22222 ± 0.00765	9.479 ± 0.703	22.906 ± 0.915	174.2 ± 8.07
Solanum laciniatum	16.262 ± 0.288	2.775 ± 0.0951	0.25604 ± 0.00928	29.868 ± 0.672	43.46 ± 1.06	419.9 ± 4.35
Vibranum tinus	7.496 ± 0.276	3.55 ± 0.166	0.4119 ± 0.0141	18.62 ± 1.35	22.152 ± 0.955	133.98 ± 1.05
F value	329.1***	405.2***	95.68***	504.8***	372.6***	66.68***
df	64	64	64	64	64	64

Species	LDMC (mg/g)	TDMC (mg/g)	SLA (cm^2/g)	LMA (mg/cm^2)	LV (cm^3)	SAV (cm^{-1})
Acacia dealbata	467 ± 22.4	466.5 ± 11.6	268.2 ± 24	3.994 ± 0.332	0.0005 ± 0.00002	82.01 ± 1.32
Acacia pravissima	431.4 ± 10	563.95 ± 6.17	93.22 ± 2.51	11.145 ± 0.321	0.0222 ± 0.00204	39.942 ± 0.941
Aesculus hippocastanum	292.9 ± 3.76	262 ± 14.7	187.2 ± 21.2	5.831 ± 0.586	1.426 ± 0.268	76.49 ± 4.31
Agathis australis	427.5 ± 15.9	364.8 ± 12.2	37.47 ± 2.08	27.34 ± 1.43	0.3939 ± 0.0567	15.813 ± 0.782
Arbutus unedo	404.24 ± 9.66	396 ± 6.54	54.65 ± 2.68	19.193 ± 0.644	0.3626 ± 0.039	30.422 ± 0.678
Aristotelia serrata	208.7 ± 10.2	245.4 ± 15.4	268.6 ± 34.3	4.262 ± 0.532	0.5953 ± 0.0723	57.91 ± 2.17
Betula pendula	378.41 ± 6.18	482.38 ± 9.72	125.92 ± 4.05	8.093 ± 0.227	0.3097 ± 0.0338	45.41 ± 1.27
Carpodetus serratus	294.91 ± 7.54	368.35 ± 6.55	158.9 ± 13.5	6.589 ± 0.617	0.2465 ± 0.0187	58.26 ± 1.78
Chamaecytisus palmensis	272.23 ± 9.41	358.73 ± 8.31	124.5 ± 20.6	9.41 ± 1.7	0.0793 ± 0.0105	40.32 ± 4.56
Choisya ternata	318.3 ± 13.1	267.3 ± 27.1	105.16 ± 8.72	9.948 ± 0.813	0.4356 ± 0.0263	30.477 ± 0.857
Coprosma propinqua	315.94 ± 9.2	386.1 ± 20.7	83.9 ± 7.34	12.63 ± 1.07	0.00557 ± 0.0004	31.548 ± 0.461
Coprosma robusta	324.9 ± 12.7	350.4 ± 20.3	89.1 ± 9.37	12.03 ± 1.07	0.857 ± 0.0731	28.55 ± 1.68
Coriaria arborea	318.19 ± 4.27	273.2 ± 10.7	99.38 ± 4.12	10.256 ± 0.432	0.6685 ± 0.0713	33.85 ± 1.35
Cytisus scoparius	192.2 ± 19.2	266 ± 19.3	158.9 ± 30.5	7.6 ± 1.01	0.01155 ± 0.0009	44.69 ± 1.42
Dacrycarpus dacrydioides	399.86 ± 8.35	469.64 ± 5.55	80.1 ± 3.16	12.823 ± 0.495	0.00093 ± 0.0001	50.37 ± 2.25
Dodonaea viscosa	314.2 ± 12.5	404.7 ± 22	111.5 ± 10.4	9.78 ± 1.06	0.2683 ± 0.0208	40.08 ± 1.26

Eucalyptus cinerea	447.82 ± 6.48	422.73 ± 8.55	49 ± 2.06	20.694 ± 0.814	0.4542 ± 0.0456	29.239 ± 0.344
Eucalyptus viminalis	448.62 ± 6.74	404.59 ± 8.61	41.22 ± 2.74	25.48 ± 1.53	0.467 ± 0.0394	28.359 ± 0.839
Fagus sylvatica	416.09 ± 4.53	535.4 ± 11.8	150.96 ± 6.76	6.864 ± 0.302	0.4352 ± 0.0262	66.313 ± 0.957
Fraxinus pennsylvanica	337.5 ± 32.2	441.9 ± 13.5	175.2 ± 14.1	6.421 ± 0.671	0.5084 ± 0.0447	53.77 ± 3
Fuchsia excorticata	160.57 ± 9.07	210 ± 28.4	174.9 ± 19.7	6.089 ± 0.617	0.4344 ± 0.032	31.5 ± 1.47
Ginkgo biloba	361.5 ± 15.2	388.4 ± 17.9	85.76 ± 7.49	12.28 ± 1.09	0.6707 ± 0.0491	29.01 ± 1.36
Griselinia littoralis	251.4 ± 11	332.4 ± 10.6	122.5 ± 13.1	9.08 ± 1.17	1.935 ± 0.13	22.36 ± 1.22
Hebe salicifolia	271.31 ± 7.2	334.1 ± 21.5	100.98 ± 2.02	10.012 ± 0.202	0.3184 ± 0.0379	35.74 ± 1.06
Hoheria angustifolia	285.1 ± 11.3	403.1 ± 10.7	147.8 ± 15.1	7.332 ± 0.843	0.0688 ± 0.00436	41.56 ± 2.61
Kunzea robusta	374.8 ± 42.5	370 ± 7.37	97.76 ± 7.66	10.841 ± 0.851	0.00287 ± 0.0001	52.851 ± 0.337
Leptospermum scoparium	427.5 ± 8.15	463.5 ± 12.6	130.13 ± 5.75	7.897 ± 0.398	0.0039 ± 0.00012	39.41 ± 1.67
Leycesteria formosa	268.59 ± 5.67	257.9 ± 24.6	152.5 ± 15.3	6.913 ± 0.555	2.049 ± 0.396	40.2 ± 1.87
Ligustrum lucidum	329.71 ± 6.22	451.3 ± 12.4	61.56 ± 5.04	17.06 ± 1.17	1.4721 ± 0.0878	23.046 ± 0.999
Liquidambar styraciflua	323.53 ± 3.22	446.34 ± 3.16	161.1 ± 12.6	7.819 ± 0.895	2.747 ± 0.158	47.176 ± 0.463
Magnolia grandiflora	363.71 ± 6.45	388.8 ± 7.03	59.83 ± 1.59	16.921 ± 0.422	4.289 ± 0.226	22.595 ± 0.786
Maytenus boaria	308.45 ± 6.18	457.83 ± 4.98	151.97 ± 9.1	6.758 ± 0.432	0.03601 ± 0.0035	44.79 ± 1.21
Melicytus ramiflorus	231.8 ± 13.6	239.33 ± 6.67	191.8 ± 14.3	5.479 ± 0.33	0.7361 ± 0.0942	47.1 ± 0.92
Myoporum laetum	199.78 ± 5.02	257.56 ± 7.5	100.65 ± 6.43	10.461 ± 0.743	0.7029 ± 0.0674	20.98 ± 1.16
Nematolepis squamea	364 ± 7.64	452.62 ± 7.72	83.73 ± 3.58	12.136 ± 0.478	0.2003 ± 0.0115	29.462 ± 0.658
Nothoagus fusca	389 ± 10.6	447.26 ± 5.96	122.7 ± 14.9	8.675 ± 0.814	0.1179 ± 0.0111	47.21 ± 2.45
Nothofagus cliffortioide	454.5 ± 16.3	467.96 ± 4.32	76.93 ± 3.57	13.258 ± 0.599	0.02411 ± 0.0019	36.69 ± 2.14
Nothofagus menziesii	496.56 ± 7.91	458.32 ± 6.25	77.4 ± 1.67	13.064 ± 0.273	0.1026 ± 0.0781	37.83 ± 1.86
Olearia paniculata	340.1 ± 10.3	312.7 ± 29.3	69.34 ± 7.69	15.32 ± 1.43	0.4775 ± 0.0259	26.36 ± 1.79
Olearia traversiorum	289.3 ± 11.8	383.44 ± 3.8	60.15 ± 5.99	17.78 ± 1.6	0.2638 ± 0.0322	20.193 ± 0.905
Pennantia corymbosa	277.1 ± 11.1	277.08 ± 7.99	128.3 ± 11.6	8.589 ± 0.803	0.398 ± 0.0355	34.75 ± 1.4
Phytolacca octandra	110.99 ± 5.09	56.78 ± 4.83	267.3 ± 17.6	3.925 ± 0.235	2.375 ± 0.377	28.871 ± 0.927
Pinus radiata	366.04 ± 4.02	412.49 ± 8.34	146.25 ± 3.06	6.946 ± 0.12	0.02488 ± 0.0009	18.617 ± 0.336
Piper excelsum	140.34 ± 1.03	123.85 ± 4.15	223.2 ± 13.4	4.859 ± 0.293	1.3578 ± 0.092	43.962 ± 0.67
Pittosporum crassifolium	355.7 ± 12.9	434.6 ± 15	46.25 ± 3.18	22.19 ± 1.44	0.5292 ± 0.0345	16.511 ± 0.561
Pittosporum eugenioides	342.15 ± 7.67	355.1 ± 11.7	131.72 ± 8.77	7.877 ± 0.465	0.7562 ± 0.0485	43.77 ± 1.34

Pittosporum tenuifolium	397.3 ± 10.2	515.34 ± 4.74	103.29 ± 8.77	10.26 ± 1.16	0.2576 ± 0.0361	39.09 ± 1.89
Plagianthus regius	258.15 ± 9.89	327.9 ± 18.5	139.6 ± 11.6	7.671 ± 0.655	0.1064 ± 0.0157	46.42 ± 2.11
Podocarpus cunninghamii	379.5 ± 14.2	378.3 ± 12.6	26.23 ± 3.32	41.1 ± 3.48	0.02784 ± 0.0023	12.408 ± 0.8
Podocarpus totara	387.69 ± 6.56	441.8 ± 24.6	56.85 ± 2.01	17.773 ± 0.631	0.03421 ± 0.0018	16.166 ± 0.58
Populus nigra	312.02 ± 7.22	402.4 ± 8.14	122.51 ± 8.92	8.71 ± 0.613	0.4976 ± 0.0226	45.03 ± 2.13
Populus trichocarpa	352.1 ± 14.8	434.9 ± 17	102.7 ± 10.4	10.44 ± 1.07	1.67 ± 0.198	38.31 ± 2.07
Protea neriifolia	370.8 ± 10.2	300.58 ± 8.12	46.31 ± 2.6	22.14 ± 1.22	1.519 ± 0.164	18.962 ± 0.596
Prumnopitys taxifolia	384.9 ± 12.6	454.98 ± 8.41	68.29 ± 3.89	15.19 ± 0.808	0.01354 ± 0.0012	21.487 ± 0.914
Prunus kanzan	393.09 ± 5.81	505 ± 3.74	96.36 ± 4.19	10.645 ± 0.401	0.9658 ± 0.0695	43.898 ± 0.769
Prunus laurocerasus	372.69 ± 4.75	395.76 ± 9.55	67.31 ± 1.61	15.071 ± 0.34	1.88 ± 0.148	27.682 ± 0.538
Pseudopanax arboreus	330.07 ± 5.7	245.6 ± 13	61.86 ± 2.42	16.59 ± 0.657	1.554 ± 0.271	23.27 ± 0.351
Pseudopanax colensoi	292.48 ± 5.97	214.81 ± 7.43	81.43 ± 4.14	12.593 ± 0.639	1.1073 ± 0.0689	26.748 ± 0.761
Pseudopanax crassifolius	318.53 ± 6.01	299.8 ± 3.56	52.63 ± 2.37	19.68 ± 1.13	1.1677 ± 0.0514	17.844 ± 0.531
Pseudowintera colorata	357.28 ± 5.85	359.98 ± 8.32	76.13 ± 8.05	14.12 ± 1.55	0.2851 ± 0.0324	34.39 ± 1.24
Quercus ilex	454.5 ± 16.8	419.93 ± 9.72	79.74 ± 8.59	13.31 ± 1.3	0.2688 ± 0.0258	36.375 ± 0.484
Quersus robur	397.93 ± 6.45	479.48 ± 5.31	129.7 ± 13.3	9.07 ± 1.06	0.7739 ± 0.0312	54.38 ± 1.68
Salix matsudana	356.7 ± 13.3	390.2 ± 19.4	111.61 ± 7.4	9.332 ± 0.738	0.212 ± 0.0203	45.37 ± 1.76
Solanum laciniatum	179.52 ± 1.6	199.35 ± 5.65	205.17 ± 7.8	5.08 ± 0.203	0.7796 ± 0.038	39.95 ± 1.56
Vibranum tinus	402.19 ± 5.49	425.9 ± 6.77	56.07 ± 2.88	18.205 ± 0.98	0.7637 ± 0.0549	24.53 ± 0.93
F value	66.44***	62.63***	39.7***	36.84***	90.48***	95.23***
df	64	64	64	64	64	64

Species	BPRP	BPSO	SMC (%)	SV (m^3)	FFM (kg/m^3)
Acacia dealbata	10 ± 0.856	3 ± 0.258	109.52 ± 3.37	0.02348 ± 0.00239	0.5835 ± 0.0257
Acacia pravissima	10.333 ± 0.615	4.333 ± 0.211	109.1 ± 4.45	0.05489 ± 0.00552	0.3706 ± 0.0322
Aesculus hippocastanum	5.333 ± 0.333	2 ± 0	160 ± 14	0.047 ± 0.0105	0.406 ± 0.0417
Agathis australis	17.333 ± 0.919	2.167 ± 0.167	132.56 ± 9.91	0.03244 ± 0.00337	0.9235 ± 0.0406
Arbutus unedo	9.33 ± 1.2	5 ± 0.258	127.09 ± 5.12	0.04365 ± 0.0029	0.6185 ± 0.0454
Aristotelia serrata	10.67 ± 1.2	2.167 ± 0.167	294.7 ± 35.3	0.01488 ± 0.00307	0.5804 ± 0.0595
Betula pendula	7.833 ± 0.703	4.5 ± 0.224	101.28 ± 5.1	0.02298 ± 0.00427	0.4487 ± 0.0328

Carpodetus serratus	11.33 ± 1.02	3 ± 0.258	198.15 ± 4.97	0.01021 ± 0.0018	0.6299 ± 0.0236
Chamaecytisus palmensis	11.17 ± 1.76	3 ± 0.447	265.06 ± 7.98	0.03801 ± 0.00296	0.53 ± 0.047
Choisya ternata	7.167 ± 0.749	2.833 ± 0.167	156.55 ± 6.88	0.02098 ± 0.00269	0.6893 ± 0.044
Coprosma propinqua	15 ± 0.683	4.333 ± 0.211	133.16 ± 5.78	0.03089 ± 0.00271	0.3197 ± 0.0163
Coprosma robusta	14 ± 1.37	2.333 ± 0.211	225.3 ± 10.1	0.02686 ± 0.00597	0.649 ± 0.0448
Coriaria arborea	10.667 ± 0.422	2.667 ± 0.211	157.3 ± 14.8	0.03364 ± 0.00574	0.5041 ± 0.0454
Cytisus scoparius	17.333 ± 0.715	4 ± 0	242 ± 13.3	0.01709 ± 0.00229	0.5104 ± 0.0536
Dacrycarpus dacrydioides	15 ± 1	4.5 ± 0.224	138.79 ± 8.44	0.03917 ± 0.00254	0.6348 ± 0.0493
Dodonaea viscosa	11 ± 1.21	4.667 ± 0.558	208.6 ± 14.6	0.03347 ± 0.00643	0.5861 ± 0.0384
Eucalyptus cinerea	7.667 ± 0.919	3.833 ± 0.167	105.42 ± 2.99	0.04322 ± 0.00445	0.5642 ± 0.0261
Eucalyptus viminalis	8.833 ± 0.792	4.667 ± 0.422	98.65 ± 4.89	0.0999 ± 0.0104	0.3222 ± 0.0318
Fagus sylvatica	8.167 ± 0.543	3 ± 0	114.04 ± 6.59	0.0218 ± 0.00175	0.4196 ± 0.0247
Fraxinus pennsylvanica	2.5 ± 0.342	2 ± 0	168.3 ± 13.5	0.038 ± 0.00578	0.5247 ± 0.0189
Fuchsia excorticata	8.167 ± 0.601	3.167 ± 0.167	424.6 ± 22.1	0.02007 ± 0.00376	0.6054 ± 0.0473
Ginkgo biloba	2.5 ± 0.224	2 ± 0	168.9 ± 14.1	0.01439 ± 0.00104	0.8704 ± 0.0425
Griselinia littoralis	10 ± 0.447	3 ± 0	250.4 ± 14.6	0.04092 ± 0.00447	0.6896 ± 0.0353
Hebe salicifolia	10 ± 0.73	3.333 ± 0.211	219.26 ± 8.24	0.04392 ± 0.00472	0.4835 ± 0.0283
Hoheria angustifolia	13.83 ± 1.4	4.167 ± 0.307	225.2 ± 12.2	0.02987 ± 0.00479	0.5904 ± 0.023
Kunzea robusta	13.333 ± 0.558	5.5 ± 0.224	107 ± 36	0.03243 ± 0.00257	0.5838 ± 0.0184
Leptospermum scoparium	12.167 ± 0.543	5 ± 0.365	76.2 ± 10.3	0.01724 ± 0.00153	0.5213 ± 0.0258
Leycesteria formosa	7.67 ± 1.05	2.167 ± 0.167	183 ± 11.4	0.02971 ± 0.00402	0.5603 ± 0.0333
Ligustrum lucidum	7.167 ± 0.477	4 ± 0.258	158.29 ± 5.5	0.04976 ± 0.00458	0.502 ± 0.0345
Liquidambar styraciflua	5.333 ± 0.211	2.667 ± 0.211	173.5 ± 11.8	0.02826 ± 0.00257	0.5957 ± 0.0319
Magnolia grandiflora	3.333 ± 0.333	6 ± 3.8	142.92 ± 7.19	0.03408 ± 0.00447	0.7506 ± 0.0438
Maytenus boaria	9.667 ± 0.333	4.167 ± 0.167	200.6 ± 22.2	0.02134 ± 0.00138	0.5974 ± 0.0402
Melicytus ramiflorus	9.833 ± 0.703	3.667 ± 0.211	285.9 ± 16.3	0.03735 ± 0.00495	0.5147 ± 0.0244
Myoporum laetum	13 ± 0.816	3.833 ± 0.167	312.3 ± 10.6	0.03748 ± 0.00378	0.5486 ± 0.0225
Nematolepis squamea	14.5 ± 0.619	3 ± 0.258	144.53 ± 5.59	0.00965 ± 0.00113	0.7066 ± 0.0447
Nothoagus fusca	12.67 ± 1.15	5.5 ± 0.224	120.62 ± 5.75	0.0241 ± 0.00342	0.6058 ± 0.051
Nothofagus cliffortioide	13.833 ± 0.792	5.5 ± 0.224	84.63 ± 1.35	0.02597 ± 0.00404	0.7149 ± 0.0519

Nothofagus menziesii	8.167 ± 0.307	5 ± 0.258	86.74 ± 5.06	0.04079 ± 0.00445	0.4774 ± 0.0918
Olearia paniculata	13.833 ± 0.654	4 ± 0.258	133.68 ± 9.99	0.0251 ± 0.00371	0.7464 ± 0.0867
Olearia traversiorum	12.83 ± 1.19	4 ± 0.258	151.4 ± 12.6	0.02035 ± 0.00294	0.7613 ± 0.0624
Pennantia corymbosa	10.333 ± 0.211	4 ± 0	325.5 ± 11.5	0.02489 ± 0.00329	0.5514 ± 0.0525
Phytolacca octandra	5.833 ± 0.477	2.833 ± 0.167	612.5 ± 35.8	0.02706 ± 0.00292	0.8009 ± 0.0628
Pinus radiata	10.167 ± 0.872	3 ± 0	145.67 ± 8.35	0.02987 ± 0.00217	0.8008 ± 0.0508
Piper excelsum	4.5 ± 0.224	3.5 ± 0.224	518.7 ± 12.7	0.01833 ± 0.00158	0.6483 ± 0.0235
Pittosporum crassifolium	9.83 ± 1.08	3.167 ± 0.307	136.74 ± 7.55	0.03491 ± 0.00634	0.7579 ± 0.0838
Pittosporum eugenioides	6.333 ± 0.422	3.167 ± 0.167	184.22 ± 8.19	0.02971 ± 0.00497	0.538 ± 0.0447
Pittosporum tenuifolium	10.83 ± 1.45	4 ± 0	152.78 ± 8.75	0.02933 ± 0.00416	0.4854 ± 0.0407
Plagianthus regius	11.167 ± 0.872	3.667 ± 0.211	187.65 ± 9.01	0.02575 ± 0.00317	0.5779 ± 0.0438
Podocarpus cunninghamii	16 ± 0.365	3.833 ± 0.167	125.78 ± 5.26	0.02024 ± 0.0035	1.0542 ± 0.0751
Podocarpus totara	16.83 ± 1.25	4.333 ± 0.211	127.92 ± 3.4	0.02696 ± 0.00248	0.7952 ± 0.0478
Populus nigra	8.5 ± 1.69	2.5 ± 0.224	195.9 ± 13.7	0.02264 ± 0.00286	0.6086 ± 0.0459
Populus trichocarpa	5.167 ± 0.307	2.833 ± 0.167	153.51 ± 5.06	0.0398 ± 0.00424	0.5941 ± 0.036
Protea neriifolia	3.833 ± 0.654	2.5 ± 0.224	139.89 ± 5.38	0.01579 ± 0.00244	1.2289 ± 0.0607
Prumnopitys taxifolia	14.5 ± 1.09	5 ± 0.258	149.96 ± 8.24	0.04012 ± 0.00513	0.5728 ± 0.0709
Prunus kanzan	11.17 ± 1.54	3.333 ± 0.211	104.38 ± 3.8	0.03325 ± 0.00259	0.6703 ± 0.0452
Prunus laurocerasus	6.833 ± 0.307	2.5 ± 0.224	157.09 ± 3.84	0.03021 ± 0.00327	0.7066 ± 0.0428
Pseudopanax arboreus	2.5 ± 0.224	2.167 ± 0.167	197 ± 14.7	0.02143 ± 0.000759	0.8187 ± 0.02
Pseudopanax colensoi	1.333 ± 0.211	2 ± 0	222.56 ± 9.71	0.0366 ± 0.00347	0.7205 ± 0.0632
Pseudopanax crassifolius	6 ± 0.365	3 ± 0	238.1 ± 15.3	0.03866 ± 0.0068	0.6235 ± 0.0557
Pseudowintera colorata	13 ± 0.775	4.333 ± 0.211	173.6 ± 17.9	0.02634 ± 0.00218	0.7383 ± 0.0508
Quercus ilex	10.33 ± 1.09	3.667 ± 0.211	93.7 ± 2.31	0.04483 ± 0.00379	0.3228 ± 0.0227
Quersus robur	7.833 ± 0.477	3.167 ± 0.167	92.7 ± 7.96	0.02969 ± 0.00255	0.4437 ± 0.0305
Salix matsudana	13.33 ± 1.17	2.333 ± 0.211	173.4 ± 11.5	0.04415 ± 0.00313	0.418 ± 0.0283
Solanum laciniatum	3.5 ± 0.224	3 ± 0	412.4 ± 56.5	0.01718 ± 0.00159	0.6365 ± 0.0339
Vibranum tinus	8.333 ± 0.615	4.333 ± 0.211	131.53 ± 1.79	0.03526 ± 0.0041	0.5078 ± 0.0502
F value	33.27***	12.32***	38.99***	10.2***	12.62***
df	64	64	64	64	64

Species	SFM (kg/m^3)	SDM (g)	FV (m^3)	FBD (kg/m^3)
Acacia dealbata	0.0533 ± 0.00417	1.78 ± 0.0389	0.010266 ± 0.000306	0.5496 ± 0.033
Acacia pravissima	0.1037 ± 0.0151	1.9872 ± 0.0443	0.03889 ± 0.00385	0.3164 ± 0.0172
Aesculus hippocastanum	0.556 ± 0.101	1.915 ± 0.051	0.01987 ± 0.00175	0.4484 ± 0.0281
Agathis australis	0.5135 ± 0.0351	2.1963 ± 0.0203	0.02726 ± 0.00276	0.5479 ± 0.043
Arbutus unedo	0.3722 ± 0.0346	2.1888 ± 0.0291	0.02183 ± 0.00276	0.6175 ± 0.0373
Aristotelia serrata	0.509 ± 0.102	1.5107 ± 0.0611	0.00925 ± 0.00171	0.4465 ± 0.0762
Betula pendula	0.2342 ± 0.0309	1.7495 ± 0.0567	0.01944 ± 0.00354	0.3734 ± 0.0305
Carpodetus serratus	0.3651 ± 0.0366	1.498 ± 0.0407	0.00958 ± 0.00137	0.3956 ± 0.0263
Chamaecytisus palmensis	0.2473 ± 0.0109	1.9188 ± 0.052	0.01899 ± 0.00185	0.4657 ± 0.0258
Choisya ternata	0.3761 ± 0.0311	1.8036 ± 0.0427	0.02614 ± 0.00417	0.3238 ± 0.0191
Coprosma propinqua	0.3468 ± 0.017	2.0554 ± 0.0539	0.02738 ± 0.00186	0.4454 ± 0.0301
Coprosma robusta	0.0451 ± 0.0105	1.8107 ± 0.0985	0.01577 ± 0.00181	0.4544 ± 0.0393
Coriaria arborea	0.3613 ± 0.0375	1.8178 ± 0.0422	0.01587 ± 0.00221	0.4603 ± 0.0457
Cytisus scoparius	0.5058 ± 0.0474	1.7419 ± 0.0525	0.00985 ± 0.00308	0.6256 ± 0.0898
Dacrycarpus dacrydioides	0.3046 ± 0.0415	1.9477 ± 0.0588	0.03351 ± 0.00229	0.3363 ± 0.0441
Dodonaea viscosa	0.2417 ± 0.0372	1.6817 ± 0.0626	0.02456 ± 0.00517	0.2963 ± 0.0397
Eucalyptus cinerea	0.1867 ± 0.042	2.1345 ± 0.0308	0.02953 ± 0.00225	0.47227 ± 0.00959
Eucalyptus viminalis	0.1506 ± 0.0226	2.1053 ± 0.0414	0.0298 ± 0.00432	0.4624 ± 0.0227
Fagus sylvatica	0.6173 ± 0.0442	1.7952 ± 0.0304	0.02337 ± 0.00314	0.3402 ± 0.0208
Fraxinus pennsylvanica	0.3042 ± 0.0443	1.8634 ± 0.0537	0.01422 ± 0.00211	0.523 ± 0.0368
Fuchsia excorticata	0.5878 ± 0.0329	1.8382 ± 0.024	0.01611 ± 0.00289	0.4824 ± 0.0508
Ginkgo biloba	0.5295 ± 0.0627	1.8459 ± 0.0546	0.007129 ± 0.000461	0.7245 ± 0.0334
Griselinia littoralis	0.4132 ± 0.0514	1.89 ± 0.0483	0.032775 ± 0.000855	0.3029 ± 0.0254
Hebe salicifolia	0.2752 ± 0.0288	1.7141 ± 0.0184	0.02487 ± 0.00155	0.2773 ± 0.0154
Hoheria angustifolia	0.0599 ± 0.00518	1.858 ± 0.051	0.02968 ± 0.0037	0.315 ± 0.0157
Kunzea robusta	0.2818 ± 0.0316	2.0462 ± 0.0273	0.02383 ± 0.00342	0.495 ± 0.0509
Leptospermum scoparium	0.2476 ± 0.0273	1.9705 ± 0.035	0.01488 ± 0.00131	0.5739 ± 0.0341
Leycesteria formosa	0.4545 ± 0.0304	1.8054 ± 0.0387	0.02282 ± 0.0045	0.3891 ± 0.0663
Ligustrum lucidum	0.3485 ± 0.038	2.0301 ± 0.0403	0.03327 ± 0.00358	0.3843 ± 0.0361

Liquidambar styraciflua	0.2097 ± 0.0155	1.5541 ± 0.0467	0.00919 ± 0.00131	0.4435 ± 0.0265
Magnolia grandiflora	0.0664 ± 0.0368	1.9849 ± 0.0336	0.03041 ± 0.00208	0.3715 ± 0.0149
Maytenus boaria	0.2153 ± 0.0262	1.6331 ± 0.0309	0.02129 ± 0.00198	0.2739 ± 0.0128
Melicytus ramiflorus	0.1862 ± 0.0167	1.564 ± 0.0439	0.02295 ± 0.00373	0.2431 ± 0.0345
Myoporum laetum	0.4309 ± 0.0363	1.8036 ± 0.0367	0.02552 ± 0.00199	0.3172 ± 0.0197
Nematolepis squamea	0.4132 ± 0.0206	1.5463 ± 0.0782	0.01104 ± 0.00122	0.3867 ± 0.0333
Nothoagus fusca	0.3984 ± 0.0354	1.9576 ± 0.0332	0.0204 ± 0.00283	0.4811 ± 0.051
Nothofagus cliffortioide	0.3515 ± 0.0355	2.0211 ± 0.0332	0.02193 ± 0.00333	0.5016 ± 0.0333
Nothofagus menziesii	0.3069 ± 0.0315	2.0378 ± 0.0246	0.02576 ± 0.00223	0.4529 ± 0.0304
Olearia paniculata	0.3745 ± 0.0403	1.9089 ± 0.0344	0.02122 ± 0.00308	0.4433 ± 0.0474
Olearia traversiorum	0.0838 ± 0.0111	1.9685 ± 0.0301	0.02318 ± 0.00267	0.4431 ± 0.0262
Pennantia corymbosa	0.557 ± 0.0338	1.7248 ± 0.0445	0.01981 ± 0.00139	0.3359 ± 0.0241
Phytolacca octandra	0.5982 ± 0.0295	1.6269 ± 0.0447	0.01094 ± 0.00197	0.4539 ± 0.051
Pinus radiata	0.4524 ± 0.0483	1.9839 ± 0.0246	0.01729 ± 0.00174	0.5373 ± 0.0241
Piper excelsum	0.5589 ± 0.0608	1.409 ± 0.0276	0.010106 ± 0.00099	0.3291 ± 0.027
Pittosporum crassifolium	0.4259 ± 0.0844	2.0151 ± 0.0556	0.02968 ± 0.00351	0.4149 ± 0.0564
Pittosporum eugenioides	0.224 ± 0.036	1.61 ± 0.0434	0.01821 ± 0.00238	0.3026 ± 0.0226
Pittosporum tenuifolium	0.0598 ± 0.00678	1.73 ± 0.0538	0.01703 ± 0.00178	0.37758 ± 0.00899
Plagianthus regius	0.3747 ± 0.0328	1.9093 ± 0.03	0.0135 ± 0.00219	0.5833 ± 0.0589
Podocarpus cunninghamii	0.6434 ± 0.074	2.1689 ± 0.0157	0.0197 ± 0.00223	0.6346 ± 0.0384
Podocarpus totara	0.3616 ± 0.0436	1.9838 ± 0.0375	0.0188 ± 0.00178	0.5142 ± 0.045
Populus nigra	0.3934 ± 0.0541	1.7468 ± 0.0314	0.00656 ± 0.00126	0.7125 ± 0.0631
Populus trichocarpa	0.5238 ± 0.0389	2.044 ± 0.0332	0.01599 ± 0.0019	0.6109 ± 0.0425
Protea neriifolia	0.844 ± 0.0407	2.1963 ± 0.057	0.01783 ± 0.00283	0.7062 ± 0.0386
Prumnopitys taxifolia	0.287 ± 0.0486	1.9857 ± 0.048	0.03401 ± 0.00425	0.351 ± 0.0187
Prunus kanzan	0.4622 ± 0.0327	2.0933 ± 0.0676	0.03466 ± 0.00529	0.4167 ± 0.0224
Prunus laurocerasus	0.431 ± 0.0385	1.8499 ± 0.00837	0.01947 ± 0.00202	0.4154 ± 0.0284
Pseudopanax arboreus	0.5423 ± 0.0356	1.8501 ± 0.036	0.01342 ± 0.00123	0.5206 ± 0.0201
Pseudopanax colensoi	0.4341 ± 0.0256	1.7895 ± 0.0582	0.011853 ± 0.000472	0.5144 ± 0.0428
Pseudopanax crassifolius	0.3756 ± 0.0323	1.7323 ± 0.046	0.01642 ± 0.00197	0.3915 ± 0.0152

Pseudowintera colorata	0.5995 ± 0.0461	2.0295 ± 0.0545	0.01973 ± 0.00277	0.54 ± 0.054
Quercus ilex	0.166 ± 0.0155	1.7231 ± 0.0296	0.01939 ± 0.00269	0.3479 ± 0.0211
Quersus robur	0.3668 ± 0.0407	1.7963 ± 0.0444	0.02087 ± 0.00177	0.3663 ± 0.0311
Salix matsudana	0.1187 ± 0.00763	1.7501 ± 0.0179	0.02768 ± 0.00295	0.2782 ± 0.0248
Solanum laciniatum	0.3798 ± 0.021	1.2912 ± 0.0601	0.010186 ± 0.000765	0.2684 ± 0.0258
Vibranum tinus	0.3339 ± 0.0285	1.9471 ± 0.0481	0.02953 ± 0.00331	0.3632 ± 0.0207
F value	17.41***	18.93***	8.426***	9.452***
df	64	64	64	64

Table S3.5 Partitioned variance (%) for each of the shoot-level flammability variables and functional traits at species and individual levels calculated from analysis of variance (ANOVA).

Flammability variable	% variance explained	
	Species	Individual
Ignition time (s)	0.94	0.06
Maximum temperature (°C)	0.77	0.23
Burn time (s)	0.79	0.21
Burnt biomass (%)	0.89	0.11
Functional trait		
Leaf length (cm)	0.98	0.02
Leaf width (cm)	0.99	0.01
Leaf thickness (mm)	0.95	0.05
Leaf area (cm^2)	0.99	0.01
Leaf perimeter (cm)	0.98	0.02
Leaf moisture content (%)	0.93	0.07
Leaf dry matter content (mg/g)	0.93	0.07
Twig dry matter content (mg/g)	0.92	0.08
Specific leaf area (cm^2/g)	0.89	0.11
Leaf volume (cm^3)	0.95	0.05
Surface area volume ratio (cm^{-1})	0.95	0.05
Branching pattern (ramification point	0.89	0.11
Branching pattern (stream order)	0.71	0.29
Shoot moisture content (%)	0.88	0.12
Shoot volume (m^3)	0.95	0.05
Foliage fraction mass (kg/m^3)	0.71	0.29
Twig fraction mass (kg/m^3)	0.83	0.17
Fuel bulk density (kg/m^3)	0.65	0.35

Chapter 4

Flammability of crown fuel mixtures is non-additive: low flammability plants reduce fire residence time and total heat release

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Author contributions

This study was conceived by TC, AA, CF, GP, and SW and designed by AA, TC, CF, GP, and SW. Samples were collected by AA, JS and PM. Analyses were conducted by AA, SW, TC, and GP. AA wrote the first draft, which was then revised and approved by all co-authors.

4.1 Abstract

1. Quantifying plant flammability is a key component of understanding the hazards and behaviour of fire in the field, and numerous studies have been undertaken to quantify the flammability of individual species. However, in nature, plants with varying flammability co-occur, and wildfires often burn through the canopy of mixed stands. Hence, experimental burning of mixed-species fuels is needed to gain knowledge of actual fire behaviour in the field where multiple species burn in combination, but there has been little research on this.

2. In this study, we measured the flammability of 70 cm shoot samples from two high-flammability and two low-flammability species, across all pairwise combinations, using oxygen depletion calorimetry. Using measurements of eight flammability variables (time to ignition, heat release rate, peak heat release rate, time to peak heat release rate, total heat released, total burn time, heat of combustion and residual mass fraction), we evaluated whether: 1) the flammability of the two-species mixtures was different from the constituent individual species, and 2) the presence of low flammability species influenced the different flammability variables in the mixed-species burns.

3. The overall flammability of the shoot-level fuel mixtures was non-additive, i.e., differed from expected flammability based on the arithmetic mean of the component species in monospecific burns, and was driven by the most flammable species. While the variables related to ignitibility and combustibility were unaffected by the presence of low flammability species in the mixed fuel (i.e. were driven by the more flammable species), the burning time and total heat released were significantly reduced by less flammable species.

4. This study shows that flammability differs in mixed-fuels to the monospecific burning of their constituent species, and is usually driven by the specific flammability of a single species in the mixture. The reduction of burning time and total heat release by the presence of low flammability species in the mixture highlight how low flammability species could be used to reduce fire spread and damage.

4.2 Introduction

When plants burn during a wildfire, they rarely burn in isolation; rather, they are consumed as part of a fuel mixture that includes co-occurring species. These co-occurring species may vary in their flammability (Dickinson & Kirkpatrick 1985; Calitz *et al.* 2015; Wyse *et al.* 2016): e.g. some species may ignite faster and burn hotter, whereas others could burn longer at relatively lower temperatures (Pausas *et al.* 2017)). These inter-specific differences in flammability, in turn, result in differences in fire behaviour (Bessie & Johnson 1995; Cumming 2001; White & Zipperer 2010). While experiments burning species separately can aid our understanding of how they can individually promote or inhibit fire (White & Zipperer 2010), it is essential to assess how species interact to affect the flammability of the overall fuel mixture, as this will provide a more realistic understanding of how vegetation burns in wildfires. Hence, experiments burning plants as fuel mixtures of co-occurring species are required (Van Altena *et al.* 2012; Wyse *et al.* 2017; Della Rocca *et al.* 2018).

In general, plants of varying flammability will burn in a fuel mixture via one of two mechanisms. Either, the flammability of the mixture will be additive, where both species have an equal impact on the combustion of the fuel, or the flammability of the mixture will be non-additive, and the high flammability (super-additive) or low flammability (sub-additive) species will dominate the burning (de Magalhaes & Schwilk 2012; Varner *et al.* 2015). Moreover, additivity or non-additivity may vary across each of the four recognised variables of flammability: ignitability, combustibility, sustainability, and consumability (Anderson 1970; Martin *et al.* 1994). Each flammability variable has different ecological and management implications; for example, sustainability will influence fire residence time, and combustibility will influence the rate of heat release from a fire. Fire residence time and the amount of heat released are directly linked to plant mortality during fire, as plants exposed to prolonged heat are more vulnerable to damage caused by penetration of heat to a plant's cambium (Bond and Van Wilgen 1996; Michaletz and Johnson 2007; Zylstra 2011). Hence, we need to evaluate how these fire characteristics vary with different vegetation composition.

Despite the importance of species composition for vegetation flammability, there has been little research into mixed-species fuels, and this has mostly considered leaf litter mixtures or leaf litter-twig mixtures (de Magalhaes & Schwilk 2012; Zhao *et al.* 2019). Generally, these studies have recorded strong deviations in flammability from those expected based on the constituent species when burnt individually (de Magalhaes & Schwilk 2012; Van Altena *et al.* 2012; Zhao

et al. 2016; Varner *et al.* 2017; Della Rocca *et al.* 2018), justifying the need to specifically examine mixed fuels. These studies on litter flammability provide important insights into fire behaviour in ecosystems where surface fires are the dominant fire-type, and where much of the fuel consumed is leaf litter or small twigs. However, in other ecosystems (e.g. North American boreal forest, Mediterranean forest, shrublands, grasslands), crown fires are the main fire type, where fires burn through the canopy at a high intensity (Kafka *et al.* 2001; Keeley *et al.* 2008; Alvarez *et al.* 2012). Studies of the leaf or litter flammability are unlikely to characterise canopy flammability (Fernandes & Cruz 2012); plant parts that retain architecture, such as shoots, will be more relevant (Perez-Harguindeguy *et al.* 2013; Schwilk 2015, Alam *et al.* 2019). However, there is a lack of research on fuel mixtures at the shoot-level.

A shoot-level, mixed-fuel study was conducted by Wyse *et al.* (2017), who burned 70 cm branches of paired species in a mixture for six indigenous and four invasive species in New Zealand. They demonstrated non-additivity in some flammability variables (i.e. super-additive: ignitibility, combustibility; sub-additive: sustainability) and concluded that overall flammability was driven by the more flammable constituent species in the mixture. Thus, Wyse *et al.* (2017) demonstrated how flammable invasive plant species might increase the flammability of an ecosystem where they invade and shift vegetation composition through vegetation-fire feedbacks (Paritsis *et al.* 2015; Perry *et al.* 2015; Padullés Cubino *et al.* 2018). However, the low-technology device that Wyse *et al.* (2017) used for burning has several limitations. Importantly, that device is open-air, which does not allow for use of oxygen depletion calorimetry, an approach which can help understand the complex behaviour of mixed fuel combustion and the physical and chemical reactions that take place during combustion (Tewarson 2002; White & Zipperer 2010). In particular, the variables such as the amount of heat release and heat release rate from burning are critical in understanding fire behaviour in the field and are extensively used in modelling fire behaviour (Rothermel 1972; Alexander 1982; Babrauskas & Peacock 1992), and these can be gleaned from oxygen depletion calorimetry (Parker 1984; Janssens 2015). Furthermore, the device used by Wyse *et al.* (2017) also employed only a single blowtorch to ignite the fuel mixture, which could result in a misestimation of the ignition time of a mixed-species sample, depending on which species was contacted first by the ignition source.

Finally, the reliance on visual estimations of burn time and burnt biomass of a fuel mixture used by Wyse *et al.* (2017) might not accurately represent sustainability and consumability, respectively. In short, an improved methodology is required to quantify the complex fire

dynamics of mixed-species fuels at the shoot-level. Therefore, we used a similar shoot-level mixed-fuel approach to Wyse *et al.* (2017) but analysed the emission of gaseous compounds during burning using a novel device (Curran *et al.* in prep.) to assess the non-additive flammability of the mixed fuels.

Burning fuel mixtures composed of varying flammability fuels will help to understand the role of specific plants in altering the overall fire behaviour during a wildfire, whereby highly flammable plants might increase the probability of landscape burning and less flammable plants might reduce the flammability of the landscape (Wyse *et al.* 2017; Padullés Cubino *et al.* 2018). The use of low flammability plants around infrastructure or in strategic locations as green firebreaks has been recommended worldwide (Curran *et al.* 2017; Murray *et al.* 2018), and is being actively used in many countries (Cui *et al.* 2019). However, little empirical research has examined how low flammability plants influence fire behaviour. Hence, burning mixed fuels will assist in assessing the specific roles of low flammability species on fire behaviour and also determine which flammability variables are mostly influenced by the presence of low flammability species. It should inform land managers as to how to reduce the impact of fires in ecosystems where that is the priority, and so help conserve fire-sensitive biodiversity.

We burned two high flammability and two low flammability species across all pairwise combinations to examine the mechanisms underpinning the combustion of mixed fuels. Using oxygen depletion calorimetry, we assessed several flammability variables (Table 4.2) known to be related to fire behaviour in the field with a purpose-built device that is able to burn 70 cm shoots of woody plants. In particular, we assessed: 1) whether the flammability of mixed fuels was non-additive or additive; and 2) how the presence of low flammability species affected the flammability in mixed-species burning. To our knowledge, this is the first time where canopy fuels have been combusted using oxygen depletion calorimetry to examine the additivity of different flammability variables.

4.3 Materials and methods

4.3.1 Study area and sample collection

Samples were collected in April and June 2017 from Hinewai Reserve (173°00'46.7"E, 43°48'59.9"S) located on the Banks Peninsula, south-east of Christchurch, New Zealand. It is a 1250 ha area situated approximately 500 m a.s.l and mainly used for ecological restoration. The climate is temperate, with an annual average rainfall of ca.1639 mm (Wilson 2013). We examined two New Zealand indigenous species (*Kunzea robusta* Myrtaceae and *Melicytus ramiflorus* Violaceae) and two exotic species (*Ulex europaeus* Fabaceae and *Cytisus scoparius* Fabaceae). These species are all woody trees or shrubs, vary in flammability (Table 4.1; Wyse *et al.* 2016) and commonly co-occur in early-mid successional communities in New Zealand. Each sample consisted of a 70 cm-long terminal branch (Jaureguiberry *et al.* 2011; Wyse *et al.* 2016). A single shoot was collected from each individual plant and 30 individual shoots were collected per species. Each individual plant was reproductively mature, healthy, and not water-stressed visually, while each shoot sample taken was done so to be considered representative of the plant. If shoots retained dead material (e.g. *U. europaeus*) this was collected as part of the sample, as it can influence shoot flammability (Dent *et al.* 2019). We did not manipulate the structure of each shoot as we wanted to retain its typical architecture. Mean mass and volume (n = 30) of samples from each species are given in Table 4.1. Samples were stored for between 1-3 days in sealed plastic bags at 4-8°C after collecting from the field.

Table 4.1 The family, origin, level of flammability, habit and average mass and volume of the species included in this study.

Species	Code	Origin	Family	Flammability category	Habit	Mean mass (g)	Mean Volume (m^3)
Kunzea robusta de Lange & Toelken	Kunzea	NZ indigenous	Myrtaceae	High	Tree	124.8 ± 8.9	0.048 ± 0.006
Ulex europaeus L.	Ulex	Exotic	Fabaceae	High	Shrub	172.9 ± 9.5	0.054 ± 0.004
Melicytus ramiflorus J.R.Forst. & G.Forst.	Melicytus	NZ indigenous	Violaceae	Low	Tree	89.07 ± 6.34	0.064 ± 0.007
Cytisus scoparius (L.) Link.	Cytisus	Exotic	Fabaceae	Low	Shrub	76.9 ± 5.6	0.027 ± 0.004

Taxonomy and indigenous range follow the Ngā Tipu Aotearoa – New Zealand Plants (see: https://www.landcareresearch.co.nz/resources/data/nzplants). Flammability category determined by Curran *et al*. unpublished.

4.3.2 Sample preparation

All samples were laid out on benches at room temperature for 24 hours before burning following the protocols of Wyse *et al.* (2016), to better match the moisture content of the samples to the ignition source (White & Zipperer 2010; Wyse *et al.* 2017). To supply the combinations of species for the fuel mixtures in this experiment, shoots were chosen randomly from the samples. Two individual samples were combined in each burning trial for the single species and mixed-species burns to ensure the fuel mass available for consumption was relatively similar. Ten species combinations (each species in combination with all the other species (six combinations), plus every single species: four) were burned, with six replicates per combination.

To calculate the moisture content of the sample at the time of burning, a small subsample between 5-10 cm length, including leaves and twigs was taken from each shoot. These subsamples were weighed for fresh mass and then oven-dried at 70°C for 72 h to determine the dry mass. Moisture content (MC; %) of the subsamples was calculated on a dry mass basis following Behm *et al.* (2004):

$$\text{MC}\ (\%) = \frac{fresh\ mass - dry\ mass}{dry\ mass} \times 100 \qquad \text{.....4.1}$$

Moisture content per burn was calculated as the weighted average of the moisture content of the two samples, based on their pre-burn weights. The weight of the samples and dimensions (maximum length, width, height) when laid in the flammability device were used to calculate the bulk density of the fuel. Bulk density (BD; kg m^{-3}) was calculated by dividing total dry biomass (kg) by volume (m^3). Dry biomass per sample was calculated from the pre-burn weight using the subsample moisture content as a calibration factor to convert fresh sample biomass to its approximate dry biomass. The volume per sample was calculated following the equation for a cone with an ellipse as its base (Equation 4.2). Bulk density was calculated for the sample used in each burning trial:

$$\text{BD}\ (\text{kgm}^{-3}) = 12 \times \frac{dry\ biomass}{\pi \times length \times width \times height} \qquad \text{.....4.2}$$

4.3.3 Description of the burning device

The experiment was carried out in a purpose-built, specialised calorimeter to burn small branches of plants (Curran *et al.* in prep.). The calorimeter consisted of an octagonal steel chamber with a hood (Fig. 4.1a) that can be closed to provide controlled conditions during burning. The smoke-sealed hood also ensured that there was no gas leakage from the system during the experiment. The internal temperature was controlled using a single premixed burner that ran the length of the chamber. Holes were drilled in the bottom of the chamber to ensure sufficient ventilation for combustion. Plant samples were placed in a metal mesh tray (Fig. 4.1b), which lay at the middle of the compartment above the burner. In addition to the gas-burner, six ignition jets acted as the ignition source for the plant material. These jets were kept on during the experiment to assist with preheating and enable calibration of the heat release curve.

During the pre-heating phase (first 120 s) the ignition jets were kept below the sample, before being raised via a lever to contact the samples. The burner and ignition jets were supplied with Liquefied Petroleum Gas (LPG). The whole structure was connected to a gas analyser (Siemens Oxymat 6 paramagnetic oxygen analyser and an Ultramat 6 NDIR analyser for CO and CO_2) (Fig. 4.1c) that measured the gases from the combustion of fuels and calculated the burning characteristics of the fuels using oxygen depletion calorimetry (ODC). The ODC method assumes a constant net amount of energy is released per unit mass of oxygen consumed (13.1 kJ/gm O_2) for complete combustion of organic solids, as outlined by Janssens (2015). During burning, the exhaust gases were extracted by a fan, through the duct (Fig. 4.1). The gases were passed through an orifice plate, with a differential pressure transducer and thermocouple used to record the pressure and temperature, to calculate the mass flow rate of the exhaust gases during the tests. Exhaust gases were then sampled through the gas analyser to measure the quantities of O_2, CO, and CO_2 given off by the burning sample. Universal Data Logger (UDL) software connected to a computer was used to record the measurements.

Figure 4.1 The calorimeter used in burning consists of a) The octagonal steel chamber, b) inside the instrument where the samples (in this case *Kunzea robusta* (lower sample) and *Ulex europaeus*) were placed, showing the wire mesh in which the sample is placed, and the burner and ignition jets used to preheat and ignite the sample, c) the gas analyser.

4.3.4 Experimental burning of plants

Before samples were placed on the device, the gas analysers were calibrated against a known gas composition of CO, CO_2, and O_2. The sealed calorimeter was preheated to 150°C, which equates to baseline conditions for these tests, based on those used for other shoot-level tests (Jaureguiberry *et al.* 2011, Wyse *et al.* 2016). A 10-minute calibration run was then carried out daily. To obtain the baseline data, the UDL was run for 60 s without any materials in the calorimeter. The shoot samples were then placed on the metal basket tray and preheated for two minutes at baseline temperature following Jaureguiberry *et al.* (2011) and Wyse *et al.* (2016); this process is an effort to imitate the radiative heat of an oncoming fire front (Jaureguiberry *et*

al. 2011; Burger & Bond 2015). The basket was positioned directly over the gas burners yet did not initially allow direct contact between the samples and ignition source, and it allowed the sample to stay intact throughout the experiment. Samples were placed horizontally and side-by-side facing the terminal side opposite to each other on the tray (Fig. 4.1b). The premixed burner and six ignition nozzles were left on below the basket in the chamber to preheat the sample. Once arranged on the tray, the maximum length, width, and height of the combined samples were measured for calculation of the sample volume and thus bulk density for the combined samples per trial. The ignition burners were then raised to ignite the sample. Once the flame had extinguished, the samples were left for a further 120 seconds to ensure there was no re-ignition.

4.3.5 Measuring flammability variables

The four flammability components: ignitibility, combustibility, sustainability, and consumability proposed by Anderson (1970) and Martin *et al.* (1994) have been expressed using different variables in different studies. Although there is a lack of a standard method for measuring these variables, a group of potential test response variables has been proposed by White and Zipperer (2010) to characterize flammability components at different levels of fuels. We used some of these variables that are most meaningful to fire behaviour in the field to characterise the burning behaviour of species mixtures of plants of varying levels of flammability (Table 4.2).

Most of the variables were estimated directly from the data logger feed (Fig. 4.2). The ignition time (ignitibility) was estimated as the time elapsed before the sample started to release heat as recorded by the heat release rate curve. Time to ignition (TTI), heat release rate (HRR), peak heat release rate (PHRR), time to peak heat release rate (TPHRR), and total heat release (THR) data for each experiment were calculated directly from the data logger (Fig. 4.2). The heat of combustion (HOC) was estimated by dividing the total heat release by the corresponding mass loss relating to effective combustion over the same period.

Table 4.2 Different flammability variables that were calculated under the four components of plant flammability**.**

Flammability component	Variables calculated in this study	Unit
Ignitibility	Time to ignition (TTI): When the samples started to release heat	s
Combustibility	Heat release rate (HRR): Amount of heat released per unit of time	kw/s
	Peak heat release rate (PHRR): Maximum amount of heat released per unit of time	kw/s
	Time to peak heat release rate (TPHRR): Time required to reach peak heat release	s
Sustainability	Total heat release (THR): Total amount of energy released during the combustion	kw
	Total burn time (TBT): Duration of time the burning continues	s
	Heat of combustion (HOC): The amount of heat released per unit mass	kw/g
Consumability	Residual mass fraction (RMF): Loss of mass during combustion compared to initial mass	%

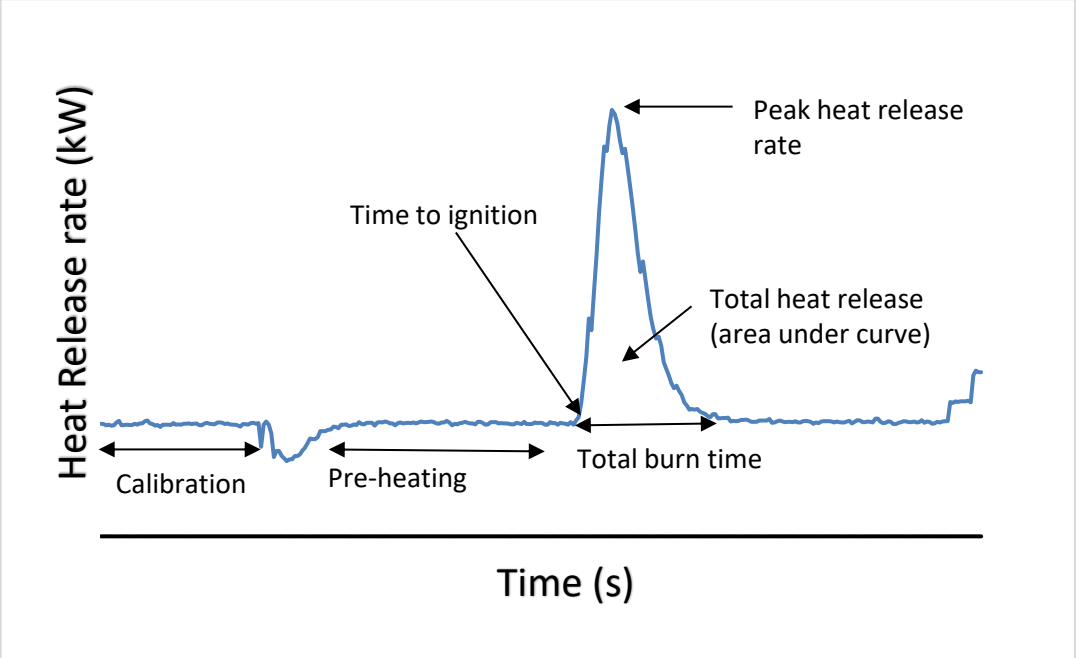

Figure 4.2 The heat release rate curve of one of the single species *Ulex europaeus* tests is shown here as an example of how the flammability variables were calculated from each burning.

4.3.6 Data analysis

We used a principal component analysis (PCA), including all the eight flammability variables from each trial to examine variation in flammability among the species and species mixtures. The first principal component score for each burning was used to calculate the non-additivity of net flammability in the species mixture because this component explained the most variation (77%) of the data. First, the mean PCA scores from the components were extracted for each species mixture and their constituent species. The flammability of each species was calculated from their respective single-species burns. Then, the Euclidean distances were calculated between the PC1 score for the mixture and the PC1 scores for each of the mixture's constituent species. The mean non-additivity in net flammability for each species combination was quantified by subtracting the Euclidean distance of the more flammable species in the mixture from that of the less flammable species in the PCA space (Wyse *et al.* 2017). These values will be zero if the net flammability of the mixed-species burn was exactly additive; otherwise, any departure from zero will indicate the non-additivity of the net flammability in the mixture. Positive values demonstrate the dominance of more flammable species, whereas negative values will demonstrate the dominance of less flammable species in the mixture. A *t*-test was performed on these values from the six species pairings to examine whether they were collectively significantly different from zero, and thus, test the hypothesis that the net flammability of mixed-species burning at shoot-level flammability is non-additive.

To assess whether each of the flammability variable was non-additive, we conducted an additional analysis of non-additivity in which the flammability variables of species mixtures were weighted by mass and volume of the constituent single species, which we considered necessary as the samples from different species in the mixture varied in their mass and volume. For the mass or volume-weighted (50:50) expectation, $\text{the expected value} = [mass\ or\ volume\ fraction\ of\ fuel\ A\ *\ flammability\ of\ fuel\ A] + [mass\ or\ volume\ fraction\ of\ \ fuel\ B\ *\ flammability\ of\ fuel\ B]$ (Van Altena *et al.* 2012). The non-additivity of each flammability variable in the species mixture burns (deviation from expected values) was assessed by comparing the observed values of the flammability variables to the expected values using a paired *t*-test. Ignition time, time to peak heat release rate, burn time, and total heat release were log-transformed to meet the assumption of normality.

To explore which constituent species drove the flammability variables of the mixtures, the contribution of each species to the flammability variables of the mixture was calculated (de

Magalhaes & Schwilk 2012). The average flammability contribution for each species in a mixture was quantified to represent how similar the behaviour of a mixture was to the behaviour of the species individually and was calculated by averaging the differences between the observed value of a mixture and that of its constituent high and low flammability species. Then, the average contribution of each species in their respective mixtures was calculated by averaging the differences between the observed value of a parameter of the mixture they present and the value of that species for all parameters. Lower values indicated that the species' individual characteristics were similar to that of the mixtures in which they occurred. Finally, all the flammability variables of highly flammable *K. robusta* and *U.europaeus* were compared with the flammability of less flammable species (*M. ramiflorus* and *C. scoparius*) and with the species mixture where they were present using a general linear model. A *post hoc* Tukey–Kramer HSD test was used to detect differences (a = 0.05) in the flammability variables between the individual species and the species mixtures. All analyses were performed using functions and routines implemented in the R software package version 3.6.1 (R Core Team, 2019).

4.4 Results

4.4.1 Variation in flammability variables among the species and the mixtures

The PCA analysis including all flammability variables showed differences in the flammability of species in isolation and in combination (Fig. 4.3, Table S4.1). The first axis of the PCA explained 77 % variation of the data and was negatively associated with all flammability variables except time to ignition and time to peak heat release rate. The loadings of all parameters were similar in the first axis (time to ignition = 0.328, heat release rate = -0.353, peak heat release rate = -0.39, time to peak heat release rate = 0.281, total burn time = -0.344, total heat release = -0.366, heat of combustion = -0.385 and residual mass fraction = -0.369). The second PCA axis explained only 8% of the variation in the data and was negatively associated with flammability variables except for heat release rate (Fig. 4.3). Peak heat release rate and heat of combustion were not related to the second axis. The PCA loadings showed that species with highly negative loadings on both of the PCA were high in flammability.

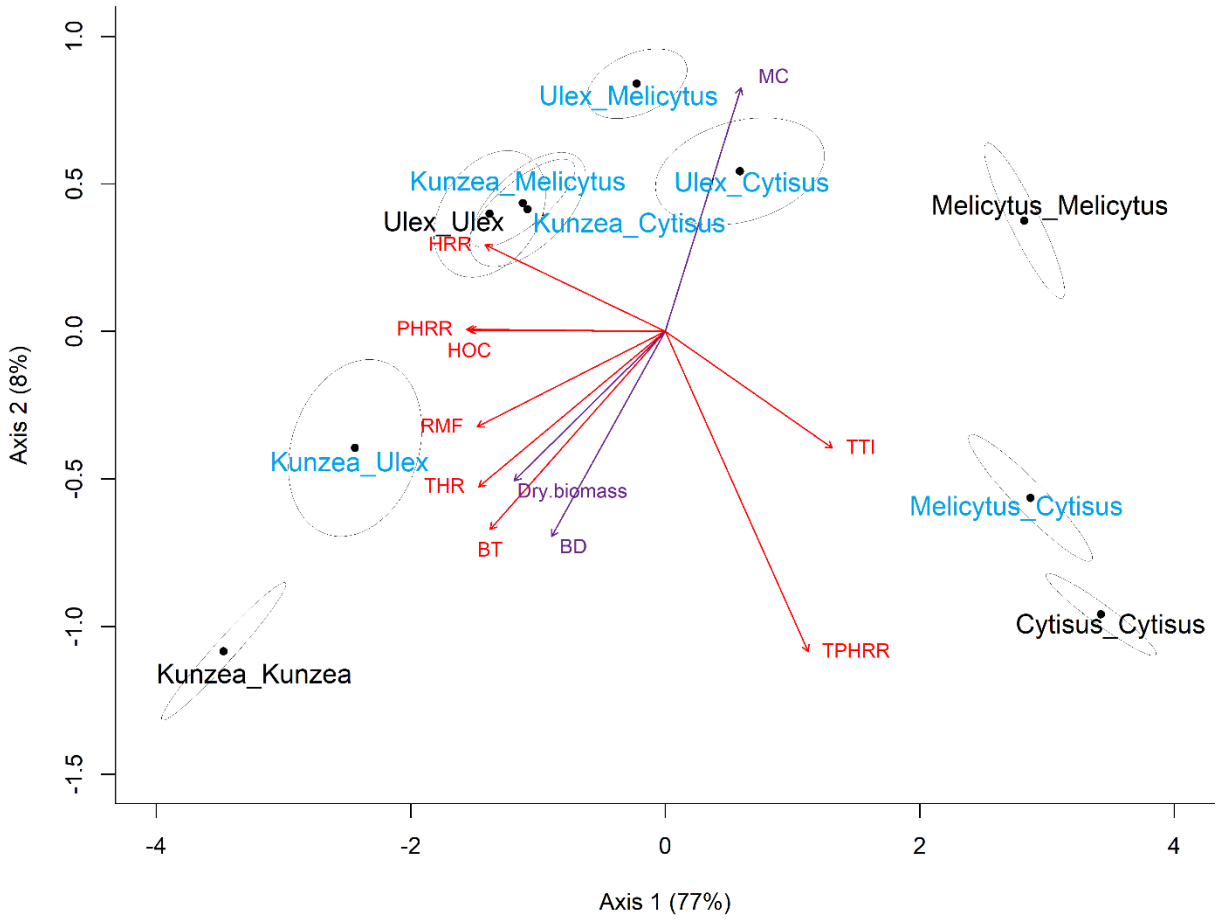

Figure 4.3 Principal components analysis (PCA) biplot of the eight flammability variables (red vectors) under study (TTI: Time to ignition; HRR: Heat release rate; PHRR: Peak heat release rate; TPHRR: Time to peak heat release rate; BT: Total burn time; THR: Total heat release; HOC: Heat of combustion; and RMF: Residual mass fraction). Points indicate the mean PCA scores per species (black vectors) and species mixtures (blue vectors) and ellipses indicate the standard error of the mean (see Table 4.1 for species codes). Purple vectors show three potential explanatory variables (dry biomass, BD: bulk density; and MC: moisture content) fitted on to the PCA scores by the *'envfit'* function from vegan (v 2.5-5) package in R (Oksanen *et al.* 2013).

Kunzea robusta was the most flammable species with the shortest ignition time, the highest amount of heat released, and it burnt longer with highest effective heat of combustion and had the highest mass loss due to burning (residual mass fraction). *Cytisus scoparius* was the least flammable with a longer ignition time, lower heat release rate, low effective heat of combustion, and a low residual mass fraction (Fig. 4.3, Table S4.1). *Ulex europaeus* had the highest heat release rate among the four species. All the explanatory variables showed a strong association with the flammability variables. Species moisture content was significantly positively

correlated (r = 0.51, P < 0.001) with PCA axis one whereas both dry biomass (r = -0.70, P < 0.001) and bulk density (r = -0.61, P < 0.001) were significantly negatively correlated with PCA axis one. Species and mixtures with high moisture content had low flammability, while those fuel mixtures with high dry biomass and bulk density had high flammability (Fig. 4.3).

4.4.2 Non-additivity among species mixtures

The PCA suggests that the net flammability of the six species-mixtures departs from the expected additive values (Fig. 4.3). The mean location of each mixed-species burn relative to its component single-species burns (Fig. 4.3), shows that the overall flammability of the mixed-species burns at shoot-level was non-additive and was driven by the more flammable species of the pairing (Table S4.3). However, not all the flammability variables were non-additive in the mixtures. When mass was used as a weighting factor, only time to ignition, total burn time and total heat release were non-additive and differed significantly from the predicted values (Table 4.3).

Table 4.3 Average non-additivity (when the difference between observed and predicted values does not equal zero) of eight flammability variables calculated from mixed-species burns.

Flammability variable	Mass-weighted	Volume weighted
	Observed-predicted	Observed-predicted
Time to ignition[ft] (s)	-3.52 ± 1.23**	-1.28 ± 0.26***
Heat release rate (kw/s)	1.11 ± 0.87	2.53 ± 0.84**
Peak heat release rate (kw/s)	2.12 ± 1.78	5.38 ± 1.98**
Time to peak heat release rate[ft] (s)	-15.27 ± 5.46**	-21.11 ± 6.20**
Total burn time[ft] (s)	-13.80 ± 3.63***	-6.65 ± 4.66
Total heat release[ft] (kw)	-108.58 ± 77.75	-165 ± 33.25**
Heat of combustion (kw/g)	0.63 ± 0.31	1.246 ± 0.384**
Residual mass fraction (%)	-3.05 ± 1.78	0.27 ± 2.20

[ft] denotes parameters that were log-transformed to meet the normality assumption. P-values (*P < 0.05, **P < 0.01, ***P < 0.001) were calculated based on paired t-test between the observed and both mass-weighted and volume-weighted predicted values. (+) means observed values of the mixtures were higher than the predicted values and (-) means observed values of the mixtures were lower than the predicted values.

In contrast, when the volume was used as the weighting factor, all the flammability variables showed significant non-additivity in the mixed-species burning, except total burn time and residual mass fraction (Table 4.3). Negative time to ignition, time to peak heat release rate, total burn time and total heat release of mixture demonstrated that the mixtures ignited more quickly and took a short time to reach peak heat release rate, burnt for a shorter period of time and released less heat.

We investigated which species drives each of the flammability variables by observing the contribution of each species to the behaviour of a mixture ('average effect in mixture'). The average effect of high and low flammable species demonstrates that the more flammable species in the mixture strongly influenced time to ignition, heat release rate, peak heat release rate, time to peak heat release rate and heat of combustion (Table 4.4).

Table 4.4 Average flammability contribution for constituent species in a mixture. This represents, on average, how close the behaviour of a mixture is to the behaviour of the individual constituent species, and it is calculated as the average difference of a flammability variable between a species and all the mixtures to which that species contributes. In bold are the lowest absolute values for each flammability variable.

Flammability parameter	High flamm-ability	Low flamm-ability	*Kunzea robusta*	*Ulex europeaus*	*Melicytus ramiflorus*	*Cytisus scoparius*
Time to ignition (s)	**0.50**	-3.6	0.55	**0.39**	-3.88	-2.27
Heat release rate (kw/s)	**-2.4**	7.1	**-1.34**	-4.53	7.46	7.81
Peak heat release rate (kw/s)	**-7.95**	18.75	-9.95	**-4.99**	19.47	17.08
Time to peak heat release rate (s)	**13.55**	-48.13	**-3.05**	8.88	8.83	-83.83
Total burn time (s)	-40.44	**29.69**	-62.06	-29.60	26.38	**22.22**
Total heat release (kw)	-812.37	**661.46**	-1139.45	**-579.31**	597.04	597.68
Heat of combustion (kw/g)	**-1.50**	4.07	-2.42	**-0.11**	3.58	4.09
Residual mass fraction (%)	-13.24	14.25	-18.70	**-2.31**	11.16	11.86

The total burn time and total heat release were mostly driven by the low flammable species in the mixture (Table 4.4). All of the studied species made different contributions to the mixtures they occurred in. *Ulex europaeus* had the smallest values for five flammability variables (Table 4.4), showing that it drove those flammability variables in the mixed-species burning where it was present. Likewise, *K. robusta* dominated time to ignition, heat release rate, and time to peak heat release rate; while *C. scoparius* strongly influenced the total burn time of the mixtures (Table 4.4).

4.4.3 Effects of low flammability plants on the flammability variables of the mixture

General linear models showed that when the low flammability species were burnt alongside more flammable species several flammability variables including total burn time, total heat release, heat of combustion and residual mass fraction were reduced significantly; on the other hand, time to ignition, heat release rate, peak release rate and time to peak heat release rate were not affected (Fig. 4.4 & 4.5). The burning characteristics of the high flammability species (*K. robusta* and *U. europaeus)* were separately analysed in the mixtures with both of the low flammability species (*M. ramiflorus* and *C. scoparius).* The mixing of low flammability species did not change the highly flammable nature of *K. robusta* and *U. europaeus* in terms of their faster ignition, high heat release rate and peak heat release rate and how fast they reached the maximum heat release rate. However, the long burn time and high heat release of *K. robusta* and *U. europaeus* were significantly reduced in the mixture with low flammability species *C. scoparius* and *M. ramiflorus*. The high heat of combustion and residual mass fraction of *K. robusta* were significantly reduced when burnt with *C. scoparius,* but not with *M. ramiflorus;* these two parameters did not change significantly when *U. europaeus* was mixed with the low flammability species (Fig. 4.4 & 4.5).

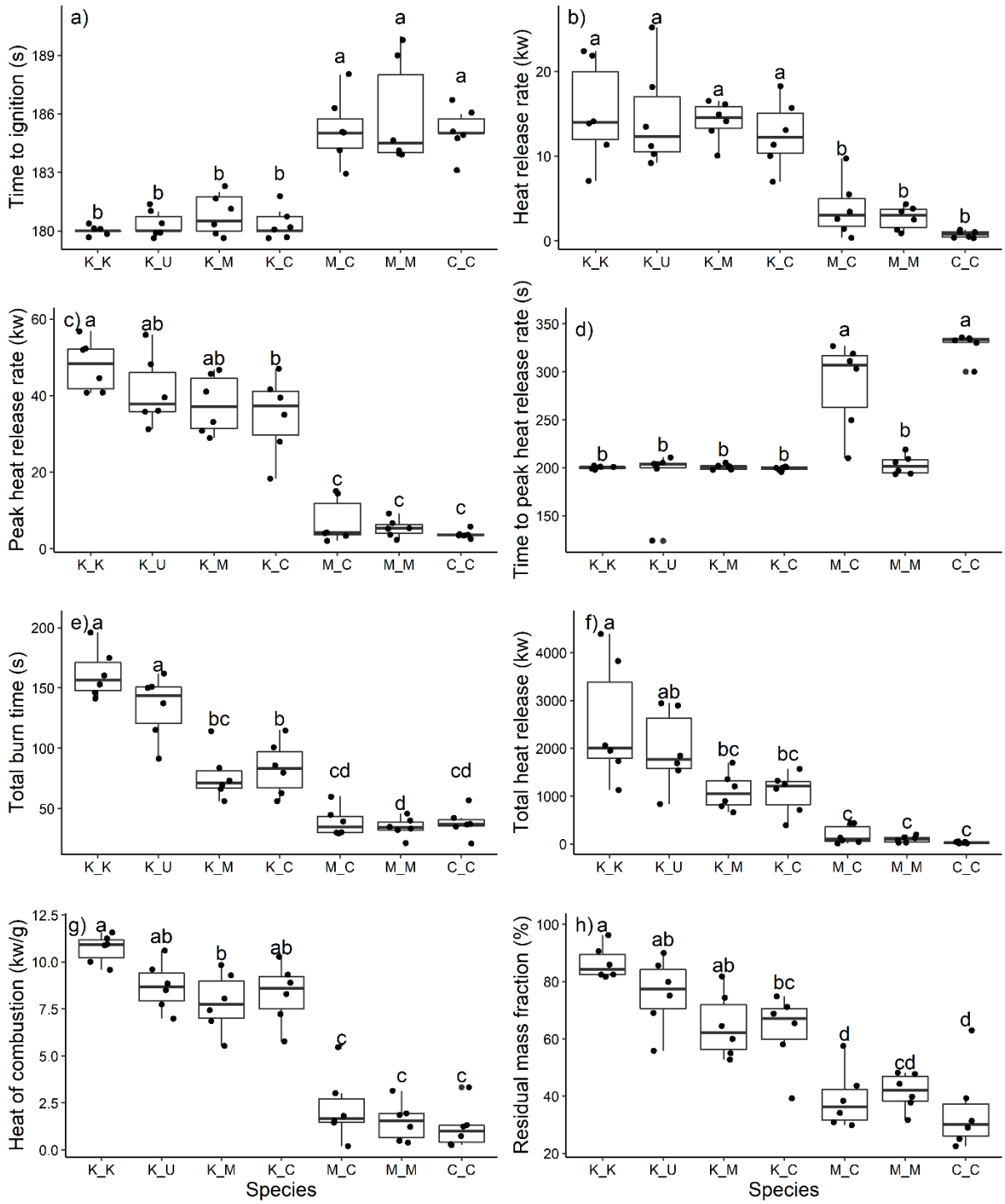

Figure 4.4 Plots comparing the flammability variables a) time to ignition, b) heat release rate, c) peak heat release rate, d) time to peak heat release rate, e) total burn time, f) total heat release, g) heat of combustion, and h) residual mass fraction of K_K (*K. robusta*) with the flammability variables of the mixture between *K. robusta* and other species: K_U (*K. robusta* + *U. europaeus*); K_M (*K. robusta* + *M. ramiflorus*); K_C (*K. robusta* + *C. scoparius*); and also, low flammability species M_M (*M. ramiflorus*), C_C (*C. scoparius*) and their mixture M_C (*M. ramiflorus* + *C. scoparius*). Different superscript letters indicate significant difference ($P < 0.05$) in post hoc Tukey test; $n = 6$.

Total burn time and total heat release were the flammability variables that were strongly affected and reduced when highly flammable species were burnt with low flammability species in the mixture, compared to when they were burnt individually. The long burning time of *K. robusta* was reduced to almost half in the mixture with low flammability species (52% with *M. ramiflorus* and 48% with *C. scoparius*) and the burning time of *U. europaeus* reduced 32% in mixture with *M. ramiflorus* and 30% with *C. scoparius* (Fig. 4.4 e & 4.5 e). Likewise, the amount of heat released from *K. robusta* was reduced by 56% and 58% when burnt in a mixture with *M. ramiflorus* and *C. scoparius,* respectively. The total heat release of *U. europaeus* reduced 46% and 58% in mixture with *M. ramiflorus* and *C. scoparius* respectively (Fig. 4.4f & 4.5f) and the heat of combustion of *K. robusta* decreased significantly in the mixture with *M. ramiflorus* and residual mass fraction reduced significantly when burnt in a mixture with *C. scoparius* (Fig. 4.4 g, h). Unexpectedly, the heat of combustion and residual mass fraction of the mixture did not differ when *U. europaeus* was burnt with low flammability species (Fig. 4.5 g, h).

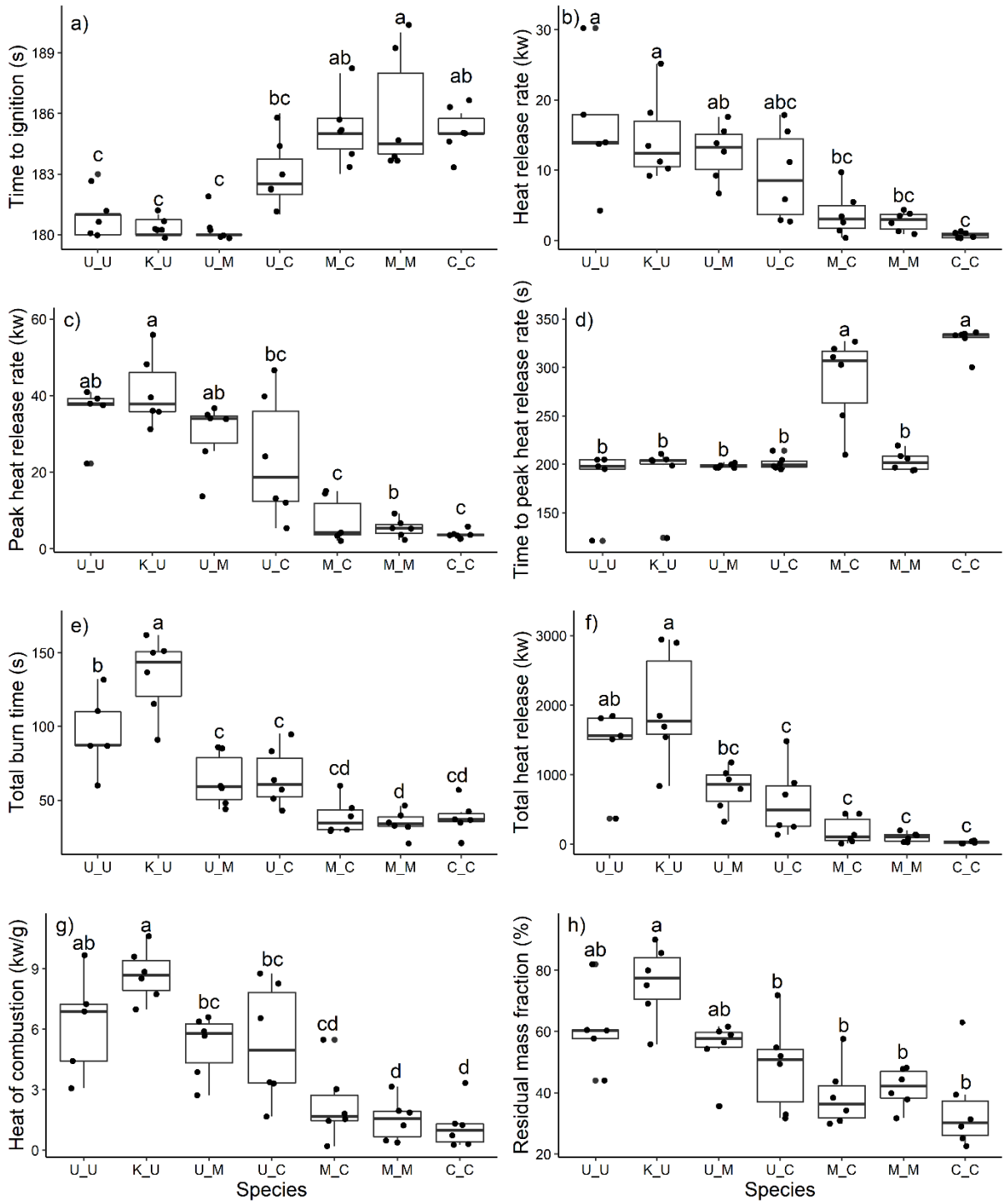

Figure 4.5 Plots comparing the flammability variables a) time to ignition, b) heat release rate, c) peak heat release rate, d) time to peak heat release rate, e) total burn time, f) total heat release, g) heat of combustion, and h) residual mass fraction of U_U (*U. europaeus*) with the flammability variables of the mixture between *U. europaeus* and other species: U_M (*U. europaeus* + *M. ramiflorus*); U_C (*U. europaeus* + *C. scoparius*); and also, low flammability species M_M (*M. ramiflorus*), C_C (*C. scoparius*) and their mixture M_C (*M. ramiflorus* + *C. scoparius*). Different superscript letters indicate significant difference ($P < 0.05$) in post hoc Tukey test; $n = 6$.

4.5 Discussion

In wildfires, plant species rarely burn in isolation; hence, it is essential to quantify the contribution of species composition on different aspects of flammability, thus providing crucial information for fire control and prevention at a time when wildfires are increasing in frequency, intensity and impact in many parts of the world (Balch *et al.* 2018; Bowman *et al.* 2018; de la Barrera *et al.* 2018). We used a novel shoot-level flammability device to demonstrate the non-additivity of flammability variables, including ignition time, heat release rate, total heat release, peak heat release rate, time to peak heat release rate and total burn time. These parameters are crucial descriptors of the combustion process, and are useful for assessing fire hazards in the field and predicting the biological effects of fire (Babrauskas & Peacock 1992; Michaletz & Johnson 2007; Schemel *et al.* 2008; Gagnon *et al.* 2010; Madrigal *et al.* 2013), and our study shows how these parameters are changed in mixed-species fuels. We demonstrate the effects of highly flammable species in fuel mixtures and how such species contribute to increasing flammability, particularly affecting the ignition time, heat release rate, and the peak heat release rate. Furthermore, we demonstrate the contribution of low flammability species' in reducing the flammability of a fuel mixture, particularly in terms of total burn time and total heat release. These outcomes help to provide a mechanistic understanding of how high flammability plants, particularly pyrophyllic invasive species, might increase the probability of fire in an invaded ecosystem (Brooks *et al.* 2004; Perry *et al.* 2014), and how low flammability plants might function as part of a green firebreak to inhibit fire spread (Curran *et al.* 2018; Cui *et al.* 2019).

4.5.1 Non-additive effects of species mixtures on shoot-level flammability

Our study adds to growing evidence that the flammability of mixed-fuels is often non-additive. Our results are broadly consistent with flammability studies conducted on leaf, litter, litter-twig, and shoot mixtures (de Magalhaes & Schwilk 2012; Van Altena *et al.* 2012; Wyse *et al.* 2017; Della Rocca *et al.* 2018; Zhao *et al.* 2019). Similar non-additive effects of species mixtures on plant flammability at different levels of fuels (leaf, litter, and shoot levels) suggest that non-additive flammability is common in both litter (leaf, twig) and canopy (shoot) fuel complexes. This understanding highlights the need to avoid viewing vegetation communities as static fuel mixtures, and instead consider them as dynamic entities that interact with and change fire behaviour (de Magalhaes & Schwilk 2012).

Only one other study has examined the additivity of mixed-species burns on canopy fuels. Wyse *et al.* (2017) burned 70-cm shoots using a low-technology device described by Jaureguiberry *et*

al. (2011) and refined by Wyse *et al.* (2016). That study also demonstrated the presence of non-additive flammability in species mixtures and showed how highly flammable invasive species may disproportionately increase the flammability of ecosystems that they invade (Wyse *et al.* 2017). While the device described by Jaureguiberry *et al.* (2011) has been recommended for the measurement of shoot flammability (Perez-Harguindeguy *et al.* 2013; Schwilk 2015) and has been widely used (e.g. Burger and Bond 2015; Calitz *et al.* 2015; Wyse *et al.* 2016, 2017; Padullés Cubino *et al.* 2018), questions remain regarding its suitability for examining the non-additivity of flammability of species mixtures. For instance, the Jaureguiberry *et al.* (2011) device has only a single blowtorch as an ignition source, which could affect the way the fire propagates through the fuel mixture. Furthermore, some of the approaches used to measure flammability variables by Wyse *et al.* (2017), such as maximum temperature reached as a measure of combustibility, and visual estimates of the proportion of sample burnt to quantify consumability, may not represent the most appropriate methods and measures of these variables of flammability.

Our novel shoot-level device (Curran *et al.* in prep) addressed each of these potential methodological shortcomings. First, our device uses six blow torches for sample ignition (Fig. 4.1b), which allows for more uniform ignition of the fuel mixture. Second, our device had the samples placed in a wire cage, which enabled measurements of mass loss due to combustion, by weighing the cage and the sample before and after burning. Third, by capturing all gases produced by the combustion process and connecting our device to an oxygen-depletion calorimeter, we obtained standard measures for combustibility, such as heat release rate, peak heat release rate, and time to peak heat release rate. Our results confirmed those of Wyse *et al.* (2017), thus validating their use of a low-technology device that allows the rapid measurement of many samples. That two studies using different measures of shoot flammability have arrived at the same conclusions suggests that our findings of non-additivity in canopy fuel mixes are robust.

4.5.2 Non-additivity of flammability variables

While the overall flammability (PC1 scores) of the species mixtures was clearly non-additive, the effect was not universal across all flammability variables. Varying degrees of non-additivity among the flammability variables of species mixtures have been observed in other mixed species flammability studies at different fuel levels (de Magalhaes and Schwilk 2012; Van Altena *et al.* 2012; Wyse *et al.* 2017; Zhao *et al.* 2019). Furthermore, the proportion of the

contribution of constituent species on degrees of non-additivity differed across the individual flammability variables, revealing the complex, multi-dimensional nature of plant flammability. This is particularly important considering that different flammability variables will each vary in their ecological impact on plants during a fire (Varner *et al.* 2015; Prior *et al*. 2017; Wyse *et al*. 2017). For instance, total burn time will reflect the residence time of a fire and therefore how long organisms will have to endure elevated temperatures, while total heat release and heat release rate relate to how much heat energy plants and animals need to withstand to survive. While plant cells can survive a short exposure above 60°C, a prolonged heat exposure below 60°C is lethal for cells (Michaletz & Johnson 2007).

The overall flammability of the fuel mixture is driven by the more flammable species, which suggests that the presence of high flammability plants will increase the overall flammability of the vegetation. However, the high flammability species in the mixture mostly drives the ignition time, heat release rate and peak heat release rate, whereas the less flammable species drives total burning time and amount of heat release in the mixture. Thus, the more flammable species exert a positive influence on the combustion process by reducing the time to ignition and increasing the heat release rate, while the less flammable species inhibit fire by reducing burning time and total heat release. While different properties of flammability are influenced by species of varying flammability in the same mixture, further experimentation is required to explore how the confounding effects of the more-flammable species on ignitibility and combustibility and the less-flammable species on sustainability and consumability interact to influence overall changes in ecosystem flammability (Wyse *et al.* 2017).

4.5.3 Low flammability species reduce the flammability of the mixture

Both the total burning time and total heat release of the mixture were driven by low flammability species in our tests. The significant reduction of burn time and total heat release due to the presence of low flammable species in the mixture suggests that less flammable species can reduce the flammability of an ecosystem. The role of low flammability species on sustainability (burn time) in a mixture was also observed in a shoot-level study by Wyse *et al.* (2017), and a leaf and litter-level study by de Magalhaes and Schwilk (2012), who described how by reducing the burning time, low flammability species affect the fire residence time of fuel mixtures. The duration of the burning of a fire is a key indicator of the effect of fire on biota. Plant survival and recovery after fire via resprouting and seed germination, survival of seed banks or rhizomes, and nutrient loss from the soil are all affected by fire residence time; i.e. how long the fire continues to burn (Kauffman *et al.* 1994; Bradstock and Auld 1995;

Brooks 2002; Vesk and Westoby 2004; Wright and Clarke 2007). Also, the burning duration and amount of heat released are associated with damage to soil microorganisms, belowground organs, and propagules, and other biodiversity adjacent to the burning areas (Michaletz and Johnson 2007; Gagnon *et al.* 2010). Therefore, by reducing both the fire residence time and the amount of heat released from fire, low flammability species in a vegetation community help change fire behaviour and can decrease plant mortality and biodiversity loss during fires (Keeley 2009; Mataix-Solera *et al.* 2009).

4.5.4 Management implications

Vegetation or fuel management is one of the priorities of forest and fire managers in the current era of extreme fires in many regions worldwide (Brackebusch 1973; Agee and Skinner 2005; Omi 2015). One of the major management implications of this study relates to the use of green firebreaks as a fire-control measure. Green firebreaks are strips of low-flammability vegetation planted at strategic locations across the landscape to slow or stop the progress of wildfires (Montgomery 1973), and have been recommended for use in many locations globally (Curran *et al.* 2018; Murray *et al.* 2018; Cui *et al.* 2019). Green firebreaks are based on the premise that low flammability vegetation can change fire behaviour and slow or even halt fires. Our study shows that low flammability fuels in a vegetation mixture with high flammability species can exert substantial influence in reducing flammability. Although green firebreaks comprised solely of low flammability species will be most effective, our study demonstrates that planting low flammability species into a community with high flammability species should also be effective by reducing the fire residence time and the amount of heat released from a fire. Both the heat released and fire residence time are not only critical for plant mortality, but also for fire managers concerned with maintaining the prescribed burning conditions required to retain sensitive ecosystem components (Wade 1993; Keeley 2009). While certain high flammability species in the landscape are vital due to their socio-cultural roles, ecological function and ecosystem services, if it is considered desirable to reduce the fire hazard in such a vegetation community, our work suggests this could be achieved by creating patches of low flammability species.

Moreover, this study emphasizes the need for careful management of highly flammable species in the ecosystem, particularly pyrophilic invasive species that increase the probability of fire of the invaded ecosystem. Invasion of pyrophilic species has increased the fire intensity of the vegetation of many ecosystems (D'Antonio & Vitousek 1992; Te Beest *et al.* 2012; Wang & Niu 2016). Our study elucidates the mechanism by which these fire- loving species, such as *U.*

europaeus, change fire regimes, by causing faster ignition and increasing the heat release rate of the vegetation. Acting as ecosystem engineer these species might cause shifts in vegetation composition through vegetation-fire feedbacks and facilitate further invasion in the invaded ecosystem (D'Antonio & Vitousek 1992; Perry *et al.* 2014; Wyse *et al.* 2017). Hence, these highly-flammable invasive species should be managed prudently considering their strong influence on ecosystem flammability. Such targeted removal of highly-flammable invasive will help fire managers to reduce the impact of fire.

Another management application of our research relates to the provision of fire refugia as a tool for biodiversity conservation and ecosystem function. Fire refugia are areas that are unburned or minimally affected by fire, which act as a reservoir of biodiversity to recolonize the post-fire landscape (Keppel *et al.* 2012; Meddens *et al.* 2018). While fire refugia operate at a variety of scales, including the landscape scale (Meddens *et al.* 2018), our findings suggest that low flammability species could provide useful refugia in a fire at the scale of an individual plant. Planting individuals of low flammability species throughout a fire-prone environment could be of great use to conservation managers when trying to protect fire-sensitive fauna with small home ranges, such as land snails (Murphy and Shea 2015). Furthermore, species with low flammability can slow down the fire front, better allowing wildlife to potentially escape the fire by moving to unburnt patches (Woinarski *et al.* 2001).

4.6 Conclusion

Our study shows that the flammability of species mixtures is non-additive at the shoot-level, suggesting that canopy fuels are disproportionately influenced by both the most and least flammable species in a mixture. Studies of leaf and litter fuels have reported similar findings (de Magalhaes and Schwilk 2012; Van Altena *et al.* 2012), suggesting that non-additive flammability may be a widespread condition for fuel mixes in nature. In shoot-level fuels, the highly-flammable species of the mixture determines how fast it will ignite and release heat, while low flammability plants regulate how long it will burn and the total heat released. This study helps to clarify the mechanisms by which high flammability and low flammability plants interact in the species mixture during the fire and how they might influence fire behaviour. Although field-based experiments are needed to determine how well these findings from controlled laboratory conditions scale up to represent those experienced during a wildfire, these findings provide an understanding of how the different canopy fuels may interact and affect the fire behaviour of mixed-species vegetation. By reducing the burning time and the amount of total heat released, low flammability plants can lessen the damage from a fire, thus highlighting the usefulness of low flammability species as a fire management tool.

4.7 Supplementary information

Table S4.1 Comparison of all the flammability variables (mean ± 1SE) measured on each species and their mixtures. *F*-values were calculated following general linear model. ****P* < 0.001.

Species	Flammability variable							
	Heat release rate (HRR) kw/s	Peak heat release rate (PHRR) kw/s	Time to peak heat release rate (t_PHRR) s	Total burn time (TBT) s	Heat of combustion (HOC) KJ/g	Total heat release (THR) kw	Residual mass fraction (RMF) %	Ignition time (IT) s
Melicytus	2.72 ± 0.57	5.43 ± 0.98	219.83 ± 20	34.50 ± 3.43	1.51 ± 0.42	100.3 ± 27.35	41.61 ± 2.61	186 ± 1.13
Kunzea	15.10 ± 2.45	47.87 ± 2.75	200.17 ± 0	161.83 ± 8.3	10.71 ± 0.31	2515 ± 525.7	86.57 ± 2.38	180 ± 0.00
Cytisus	0.76 ± 0.17	4.80 ± 1.41	313 ± 20	41.50 ± 7.67	1.20 ± 0.46	29.47 ± 6.81	38.38 ± 9.23	185 ± 0.54
Ulex	16.70 ± 3.50	36.47 ± 2.91	188.17 ± 13	94.33 ± 9.95	6.52 ± 0.98	1484.7 ± 230	62.03 ± 5.10	180 ± 0.48
Melicytus_Ulex	12.59 ± 1.65	29.79 ± 3.59	198.50 ± 0	63.50 ± 7.37	5.19 ± 0.63	800.26 ± 128	54.47 ± 3.92	180 ± 0.33
Melicytus_Cytisus	3.83 ± 1.38	7.22 ± 2.40	286.67 ± 18	42.17 ± 8.00	2.25 ± 0.74	189.73 ± 80	39.08 ± 4.24	185 ± 0.70
Melicytus _ Kunzea	14.13 ± 0.97	37.71 ± 3.17	200.83 ± 1	77.00 ± 8.29	7.83 ± 0.65	1102.2 ± 159	64.76 ± 4.64	180 ± 0.40
Kunzea _ Ulex	14.58 ± 2.72	41.11 ± 3.75	191.17 ± 13	134.33 ± 10	8.71 ± 0.53	1958.7 ± 334	75.92 ± 5.03	180 ± 0.21
Kunzea _ Cytisus	12.56 ± 1.65	34.91 ± 4.23	199.33 ± 0	83.50 ± 9.12	8.30 ± 0.65	1067.7 ± 177	62.91 ± 5.28	180 ± 0.34
Ulex _ Cytisus	9.32 ± 2.66	23.52 ± 6.75	201.50 ± 2	65.50 ± 8.10	5.32 ± 1.20	623.95 ± 208	48.76 ± 6.13	183 ± 0.73
F-value	8.27***	20.14***	12.05***	24.57***	21.57***	11.88***	9.61***	16.88***
df	9	9	9	9	9	9	9	9

See Table 4.1 for species codes

Table S4.2 Factor loadings from the principal components analysis (PCA) of all the flammability variables of all the studied species and their mixtures.

Variables	PCA axis 1	PCA axis 2
Time to ignition	0.328	-0.263
Heat release rate	-0.353	0.195
Peak heat release rate	-0.39	
Time to peak heat release rate	0.281	-0.723
Total burn time	-0.344	-0.447
Total heat release	-0.366	-0.351
Heat of combustion	-0.385	
Residual mass fraction	-0.369	-0.215
Variation (%)	77	8

Table S4.3 Significant non-addivity of flammability among species mixtures. Values are taken from the first principal component.

Species mixture	Distance to high flammability species	Distance to low flammability species	Degree of non-additivity ($\neq 0$)	*t*-test
Melicytus_Cytisus	-0.0465619	0.5550483	0.6016102	($t = 4.19$,
Kunzea_Melicytus	-2.3502143	3.9414676	6.2916819	$df = 5$,
Kunzea_Ulex	-1.0321572	1.0578511	2.0900083	$P < 0.01$)
Kunzea_Cytisus	-2.3876861	4.505606	6.8932921	
Ulex_Cytisus	-1.965756	2.8375278	4.8032838	
Ulex_Melicytus	-1.1559256	3.045748	4.2016736	

See Table 4.1 for species codes

Chapter 5
General discussion and Conclusion

The primary goal of this thesis was to better understand plant flammability and identify suites of functional traits that can determine how well plants burn. To achieve this goal specifically, I investigated the following six questions in *Chapters 2-4*:

Q1) How do flammability measurements vary between the leaf and shoot levels and which of these is a better way to measure plant flammability?

Q2) How do leaf-level morphological and chemical traits affect shoot flammability?

Q3) How do leaf functional traits and fuel architectural traits affect shoot flammability?

Q4) Can we predict shoot flammability from functional traits?

Q5) How does flammability vary in shoot-level mixed-fuels combustion?

Q6) What are the roles of the constituent species in mixed-fuel combustion?

In this chapter, I will synthesise the findings from these questions and discuss them in the light of the broader literature, specifically to clarify how this advances our understanding of plant flammability and to address how this research can be applied to large-scale vegetation and fire management planning. I will also discuss some limitations of this study and propose future research directions.

5.1 What is the best way to efficiently measure plant flammability?

The most striking result to emerge from this study is that flammability measurements conducted on shoot-level fuels can better represent the flammability of plants observed in the field than flammability measurements conducted at the leaf-level (*Chapter 2*; Alam *et al.* 2019). This result has important implications for future research aimed at developing surrogate measures of the whole plant or vegetation flammability. Estimating how plants burn during a wildfire has always been a complex task for scientists due to various factors involved in the combustion process. Knowledge on how a plant will burn during a wildfire is critical to understand the

behaviour of fire, the associated damage caused by fire, and how to plan for fire management in the future. While experimental burning using whole plants or vegetation in the field provides the best information of how fire behaves when burning through fuel, such experiments are complex to manage, expensive and sometimes dangerous to undertake, and hard to repeat. Moreover, because of the need for expensive equipment and difficulties in the transportation of large samples, very few flammability studies have been carried out at the whole plant level (e.g. Stephens *et al.* 1993; Etlinger & Beall 2005). Hence, most researchers use small plant components (leaf, litter, twig, bark, and shoot) to measure flammability and then assume that this represents whole-plant flammability.

However, measuring the flammability of a plant in the laboratory has been questioned due to the variation of flammability in different components of the plant, and the complex interaction of flammability with factors such as plant size and age, moisture content and plant architecture (White & Zipperer 2010). Also, seasonal changes affect some key traits, such as moisture content, that directly affect flammability and makes it difficult to determine the flammability of plant in the laboratory (Añón *et al.* 1995). Among different plant components, leaves are most commonly used in laboratory-based flammability studies because leaves are the first plant component to ignite during fire and are generally more flammable than other components of the plant (Midgley *et al.* 2011; Murray *et al.* 2013; Belcher 2016). However, leaf-level tests cannot represent the architecture of the plant, raising the question of how well they represent the flammability of larger plant components (Fernandes & Cruz 2012). In response to this, a device was designed to measure shoot flammability, which preserves the architecture of the plant (Jaureguiberry *et al.* 2011). While this approach has now been used in a wide range of locations (Burger & Bond 2015; Calitz *et al.* 2015; Wyse *et al.* 2016; Battersby *et al.* 2017; Padullés Cubino *et al.* 2018; Santacruz-García *et al.* 2019), there is a lack of studies which compare different flammability measurements across fuel levels and an absence of a standard way of characterising plant flammability (White & Zipperer 2010).

To help address this gap, I compared the flammability of leaf- and shoot-level fuels using data of 43 species from New Zealand to examine how they differ, and to determine which of these is best to represent the flammability of plants in the field (*Chapter 2*; Alam *et al.* 2019). This test showed that the flammability measurements between these two fuels were completely uncorrelated with each other; species showing low flammability at leaf-level were highly flammable at shoot-level. This finding is consistent with the suggestion that small components of the plant burn differently to larger components which retain architecture (White & Zipperer

2010; Varner *et al.* 2015). Both leaf and shoot fuels are extensively used in laboratory-based flammability experiments, but the question remains: which one best represents the flammability of whole plants during the fire? To assess this, I compared the flammability rankings obtained using these two fuels with the flammability rankings of plants derived from experts making observations of fires in the field (*Chapter 2*). I found that field-level expert-derived flammability rankings were correlated with the flammability of plants measured at the shoot-level, but were not correlated with leaf-level flammability. This result suggests that we have to be careful when extrapolating the flammability measurements using small plant components to whole-plant flammability. Poor correlations between whole plant flammability and flammability of small plant components (i.e., leaves) has been shown in some laboratory burning experiments (Weise *et al.* 2005; Madrigal *et al.* 2012), and has been used to argue that flammability of small plant components is not always representative of whole-plant flammability (Fernandes & Cruz 2012; Schwilk 2015).

However, my study has shown that laboratory-based flammability experiments using plant shoots as fuel can be used to estimate whole-plant flammability in the field. Moreover, this thesis provides further experimental evidence supporting the suggestion of Pérez-Harguindeguy *et al.* (2013) and Schwilk (2015) that shoot-level flammability measurements could be a standard way of measuring plant flammability, at least for canopy fuels (but not litter fuels). While studying burns of single leaves in the laboratory provides useful information on the intrinsic flammability of leaf tissues, it does not necessarily reflect how fire burns through the leaves or branches. In contrast, a shoot contains multiple leaves and twigs, preserving the architecture of a plant and so it is more likely to be representative of how fire burns through branches on a plant. This disconnect between leaf- and shoot-level flammability is a crucial finding for the field of fire ecology and suggests that we need to focus on the shoot-level or larger (whole branch, whole plant) when looking to scale up information on flammability from laboratory to the field.

5.2 Relationships between plant functional traits and flammability at the shoot-level

Plant flammability and functional traits are strongly linked with each other, and plants with different functional traits burn differently. The functional traits associated with flammability will vary depending on the fuel used for burning. For instance, leaf dimensions, leaf water content and leaf chemistry are the main contributors of leaf flammability, whereas, for large plant components or whole plants, both leaf traits and how the leaves are arranged on the branches (i.e. the fuel architecture) will influence flammability. Because leaves are commonly used in laboratory-based experiments, trait-flammability relationships at the leaf-level are well studied. In *Chapter 2*, I have demonstrated that shoot-level flammability can better represent whole plant flammability than leaf-level flammability. Therefore, an understanding of the influence of functional traits on shoot-level flammability will likely provide useful insights into how plants burn. Furthermore, as shoot samples contain leaves and twigs and preserve the architecture of the plants, this enabled me, for the first time globally, to examine the effects of multiple quantitatively measured traits (i.e. leaf traits, architectural traits) on flammability.

First, the influence of leaf morphological and chemical traits on shoot-level flammability was explored using species-level trait means from databases to establish whether the strong trait-flammability relationships identified at the leaf-level can be found at the shoot-level (*Chapter 2*). This answered *Q2* and showed that some leaf traits such as LDMC, leaf thickness, leaf phenolics, and leaf lignin were correlated to shoot-level flammability. Both the LDMC and lignin content were significantly positively correlated to all the flammability variables, suggesting that species with high LDMC and leaf lignin content were highly flammable. Leaf thickness was negatively associated with ignition percentage, and leaf phenolic concentration was significantly positively associated with the maximum temperature released during burning. Contrary to other flammability studies at the leaf-level (Murray *et al.* 2013; Grootemaat *et al.* 2015; Ganteaume 2018; Krix & Murray 2018), leaf dimensions such as leaf length, width, and area, and other leaf traits such as SLA and SAV were not related to shoot-level flammability. Moreover, the relationship between shoot-level flammability and LDMC and leaf lignin was opposite to the relationship observed at leaf-level (Mason *et al.* 2016). These contradictory trait-flammability findings between two different levels of fuels further support the conclusions from *Q1* (*Chapter 2*) that the mechanisms determining how these fuels burn are different.

However, the trait-flammability relationships in *Chapter 2* were found using species-level mean data from trait databases and published literature where the leaf functional traits and shoot-flammability variables were collected from different individuals of the species. Hence, the question remains: do these leaf traits influence shoot flammability when the traits and flammability were measured on the same individual plants? Also, given a shoot preserves the architecture of the plant, what influence do architectural traits have on shoot flammability? To tackle *Q3*, I measured the leaf traits, architectural traits and flammability of 65 trees and shrubs commonly growing in forests, farms, and gardens in New Zealand (*Chapter 3*). Again, LDMC emerged as the most important of the leaf and architectural traits in explaining shoot-level flammability, and species with high LDMC were highly flammable. Both LDMC and leaf thickness were significant predictors of flammability, further supporting the findings from *Q2* in *Chapter 2* and highlighting the potential usefulness of trait data from databases in predicting plant flammability. While LDMC is widely recognised as a useful indicator of plant strategies, plant resource use, relative growth rate, conservation of nutrients, and soil fertility (Wilson *et al.* 1999; Ryser & Urbas 2000; Garnier *et al.* 2001; Hodgson *et al.* 2011), this study establishes it as a potential predictor of plant flammability too. Moreover, the strong correlation between LDMC and other water-related traits such as leaf moisture content, shoot moisture content, and twig dry matter content reinforces the importance of fuel moisture content as a driver of plant flammability. The moisture content of fuel has already been found to be strongly negatively related to flammability and is extensively used in fire behaviour models (Pompe & Vines 1966; Rothermel 1972; Dimitrakopoulos & Papaioannou 2001; Chuvieco *et al.* 2009).

Furthermore, this study examined the role of fuel architecture on flammability and demonstrated that architectural traits such as branching pattern (number of ramifications and sub-branches) were strongly linked to shoot-level flammability; shoots with more closely-arranged branches and more fine branches were more flammable (*Chapter 3*). This finding supports the idea that plants having closely-arranged fine branches burn intensely for longer during wildfires, as having more branches increases fuel connectivity and continuity (Miller & Urban 2000). High foliage and twig fraction mass and fuel bulk density also increased shoot-level flammability indicating how the biomass of available fuel influences the burning. Fuel connectivity is vital for the fire to propagate (Green 1983; Miller & Urban 2000), and branches closer to ground connect the tree crown with the surface fuels, and more aerial branches connect one plant to adjacent plants in the canopy. Spatial connectivity of fuel in the landscape can facilitate fire spread and increase the probability of extreme fires (Allen 2007; Falk *et al.* 2007; O'Donnell *et al.* 2011). Also, species with fine and highly-branched canopies consist of closely-

spaced leaves and twigs, which provides efficient heat transfer and ensures they burn intensely for longer (Schwilk 2015).

The shoot-level trait-flammability relationships provide important information to understand the influence of functional traits on flammability and to identify some key traits in determining shoot flammability (*Chapter 2 & 3*). Considering the strong influence of functional traits on shoot flammability, I further attempted to build trait models combining both the leaf and architectural traits, with the aim of predicting shoot flammability. Among several plausible models, I found that the full model, including all the leaf and architectural traits, was the best model to predict each of the four flammability variables (*Chapter 3*). I was unable to find any more-parsimonious models with fewer traits, or models that included only easy-to-measure traits, that could adequately predict shoot flammability, further emphasising the complex nature of flammability and highlighting that it is likely driven by suites of many traits. Given that it is time-consuming to measure many of these functional traits (particularly the architectural ones), it will likely be most efficient to simply burn shoots to directly measure flammability, rather than try and predict it from traits, for species that have rarely been studied. However, when sufficient traits are known for a given species, my work has demonstrated that these can be used to predict shoot-flammability.

5.3 Flammability of mixed-species fuels at shoot-level

Chapters 2 and 3 provide clear insights on how to better quantify flammability and demonstrate the role of plant functional traits in explaining how well plants burn. I used single shoot samples for burning in both of these chapters, providing useful knowledge of the flammability of individual species, which can be used for selecting and managing vegetation to combat wildfires. However, in nature, vegetation is usually composed of multiple species and fires burn through the canopy of species with varying flammability. Therefore, it is important to understand how the flammability of mixed-fuels of different levels of flammability behaves during a fire. While we know how a low or high flammability species burns during fire, we have much less knowledge on how fuel mixtures of varying flammability burn. During mixed-species burning, both species might have an equal impact on the combustion of the fuel (additive), or the flammability of the mixture will be non-additive, and the high flammability or low flammability species will dominate the burning (de Magalhaes & Schwilk 2012; Varner *et al.* 2015).

In *Chapter 4*, I used shoot samples from four commonly co-occurring species in New Zealand and burned them in all pairwise combinations to investigate whether the flammability of mixed fuels was non-additive or additive (*Q5*); and how the presence of low flammability plants affects the flammability in mixed-species burning (*Q6*). I found that the flammability of mixed fuels was non-additive (i.e. disproportionately influenced by the flammability of the constituent species) and was dominated by the more flammable species in the mixture. This finding was consistent with flammability studies conducted at leaf-, litter- and shoot-levels (de Magalhaes & Schwilk 2012; Van Altena *et al.* 2012; Wyse *et al.* 2017; Della Rocca *et al.* 2018; Zhao *et al.* 2019), suggesting that non-additive flammability is a common attribute of different fuels and should be considered carefully when managing vegetation that is composed of species with different flammability.

Furthermore, I showed that the flammability variables such as ignition time and heat release rate of the fuel mixture were driven by the highly flammable species, whereas burn time and total heat release were driven by the low flammability species (*Chapter 4*). This is consistent with the findings of Wyse *et al.* (2017) who showed that ignition time and maximum temperature of fuel mixtures was dominated by highly flammable species and burn time was dominated by low flammability species in the fuel mixture. The ability of high flammability plants to increase the ignitibility and combustibility of the mixture highlights the mechanism by which species with high flammability, particularly pyrophilic invasive species, increase the flammability of vegetation that they invade. Such species have been found to influence the flammability of many different ecosystems globally (D'Antonio & Vitousek 1992; Te Beest *et al.* 2012; Wang & Niu 2016). Moreover, thorough vegetation-fire feedbacks these species can be favoured by the fire and may lead to changes in community composition and changes in the ecosystem state (Pauchard *et al.* 2008; Pausas 2015).

On the other hand, low flammability plants significantly reduced the burn time and total heat release from the burning of fuel mixtures. This provides laboratory support for the effectiveness of establishing green firebreaks composed of low flammability plants in strategic locations to reduce the damage caused by a fire. With increasing extreme wildfires and associated threat to human lives, properties and biodiversity (de la Barrera *et al.* 2018; Nauslar *et al.* 2018; Coogan *et al.* 2019), green firebreaks have been widely recommended as one tool to help mitigate wildfires (Curran *et al.* 2018; Murray *et al.* 2018). While field-based experimental burns are the best way to test the effectiveness of green firebreaks (Cui *et al.* 2019), this chapter provides an

understanding of the mechanisms by which low flammability species, even in a mixture with high flammability species, can help in reducing the intensity and duration of a fire.

5.4 Management implications

In this era of extreme wildfires, the findings from this thesis have important implications in terms of fire and vegetation management. In *Chapter 2*, I demonstrated that shoot-level flammability measurements are better than leaf-level tests in determining how whole plants burn during a wildfire. It has long been debated as to how best quantify the flammability of plants, and most research has been conducted on small plant components in the laboratory, that does not adequately reflect the flammability of plants in the field (White & Zipperer 2010). This thesis suggests that burning 70 cm-long shoots can be a standard way of estimating plant flammability. The way that fire burns through twigs and leaves on a shoot may also represent how fire burns through branches on a plant. The development of fire ecology and evolutionary studies requires a standard way of testing the flammability of plants (Weise *et al.* 2005). This study has helped to fulfil that goal and will allow researchers from different regions working on plant flammability in different biomes to compare and exchange their findings (White & Zipperer 2010).

Furthermore, with the risks posed by wildfire to human lives and property, particularly at the wildland-urban interface, many countries are undertaking steps to apply fire-wise planning to suppress or reduce damage from wildfire. Managing vegetation, especially around infrastructure, is a key part of this process, which involves the selection of low flammability plant species, which is dependent on having a suitable way to measure plant flammability. Additionally, mapping fire hazards based on vegetation composition is another aspect of managing wildfires across the landscape (Keane *et al.* 2000; Keane *et al.* 2001; Fang *et al.* 2018; Syphard *et al.* 2018). Proper quantification of plant flammability using shoot-level tests will help to identify which species and vegetation types are potential fire hazards and allow the implementation of appropriate fuel management plans.

From *Chapters 2 & 3*, the influence of different functional traits on shoot-flammability further facilitates a better understanding of flammability and identifies why plants with certain functional traits burn better than others. The strong association between some traits and flammability, such as LDMC, can potentially be used as a useful surrogate of shoot flammability. The similar findings for trait-flammability relationships when using either data

from databases and data measured on the same individuals that were tested for flammability shows the usefulness of readily-available trait data from global databases to characterise the flammability of species and use in modelling vegetation flammability globally. Traits such as LDMC, which is highly related to flammability and has been measured for a large number of species can easily be used to characterise the flammability of many species globally. Also, the strong association between traits associated with fuel moisture content and flammability provides further experimental support for the idea of predicting landscape fire behaviour via large-scale estimation of vegetation moisture content through remote sensing and global mapping of vegetation moisture content.

My findings regarding the importance of fuel architecture in driving shoot-level flammability are relevant to the management of fuels around homes and property. Fuel biomass, connectivity, and continuity are vital for the fire to propagate (Green 1983; Miller & Urban 2000), and branches closer to the ground connect the tree crown with the surface fuels, while having more aerial branches connect one plant with another. High spatial fuel connectivity can facilitate fire spread across the landscape and increase the potential for large fires (Allen 2007; Falk *et al.* 2007; O'Donnell *et al.* 2011). The strong influence of fuel architecture, such as branching pattern and fuel bulk density, on combustibility and spread in a shoot provides empirical support for the value of mechanical fuel management to reduce fuel loadings and to disrupt fuel connectivity, hence reducing the impacts of fire.

Finally, this study demonstrates how low flammability plants can function to reduce the damage caused by fire (*Chapter 4*). Selection of low flammability plants and their use in green firebreaks, specifically in the wildland-urban interface, or any strategic locations across the landscape such as roadsides, farm edges and adjacent to houses or other infrastructure, can be useful to reduce the impacts of fire (Cui *et al.* 2019). Given the tremendous loss of many lives, massive damage to infrastructure and impacts on biodiversity caused by catastrophic fires in many parts of the world (e.g. USA, Greece, Portugal, and Chile), further fuel and vegetation management is needed. Before establishing reforestation programs or timber plantations we have to consider that the species planted represent potential fuel for fires, and we should carefully plan to avoid planting highly flammable species in areas where they increase the fire hazard to unacceptable levels. We should also consider planting low flammability vegetation that can work as green fire breaks to provide protection from fire and reduce fire spread across the landscape. Although there are no fire-proof plants and with suitably extreme weather every plant will burn, this thesis clearly demonstrates that there are some plants that are less

flammable than others and which can be appropriate for fire-wise landscaping around homes and infrastructure.

5.5 Future research directions

This thesis has provided information that improves our understanding of plant flammability and will thus contribute to better fire and vegetation management planning. However, throughout this research project, questions arose that need further attention to improve the findings and which could potentially be included in future shoot-level plant flammability studies.

This thesis emphasises the strong trait-flammability relationship at shoot-level fuel and demonstrates how plants with certain combinations of functional traits burn more intensely than others (*Chapter 2 & 3*). While I measured all the functional traits manually for the leaf and shoot, it was time-consuming, and for some traits (i.e. shoot volume or fuel bulk density) the estimation was less precise. Functional trait measurement of the shoot through 3D images using photogrammetry (Kędra *et al.* 2019; Paulus 2019) is a promising way to easily obtain precise and reliable trait information, particularly on leaf dimensions and shoot architecture. Future work should focus on this to develop an easy and efficient way of measuring the functional traits of plant shoots from digital images. This should save time and effort and further improve our understanding of trait-flammability relationships, particularly those related to architectural traits.

Trait-flammability relationships in this thesis were examined using species grown in New Zealand (*Chapter 2 & 3*), which is, for the most part, not a fire-prone region (Ogden *et al.* 1998; Perry *et al.* 2014). While a number of species studied in this thesis are introduced from fire-prone regions of the world, it will be useful to examine the trait-flammability relationships focussing on species from regions with frequent fire, and intense weather conducive to extreme wildfires such as Mediterranean Europe, Australia, and the USA, to determine if there is variation in trait-flammability relationships across regions with different fire regimes.

The flammability variables measured by the main device used in this thesis (*Chapter 2 & 3*) provided vital information on the burning of shoots. However, measuring other variables, such as flame height and heat release rate (HRR) would be useful for further improving our understanding of plant flammability. Both flame height and HRR are considered highly relevant to the fire behaviour in the field and provide insights on fire spread and damage caused by fire.

Future shoot-level flammability studies should examine these variables to better allow for upscaling of shoot-level flammability to field-level plant flammability. Flame height could easily be measured on the device designed by Jaureguiberry *et al.* (2011) by removing the hood used as a windbreak and burning samples indoors under a fuel hood. Heat release rate requires a more specialised device to be measured, such as the enclosed device attached to a calorimeter used in *Chapter 4*.

In the trait-flammability model (*Chapter 3*), I included leaf morphology and fuel architectural traits to predict shoot flammability. For completeness, it would be good to include chemical traits (e.g. leaf phenolic, tannins, and terpenes) along with leaf and architectural traits to improve the prediction, as leaf chemicals are strongly linked with the flammability of plant (*Chapter 2*; White & Zipperer 2010; Pausas *et al.* 2016). However, they can be expensive to measure on high numbers of replicates of individuals and species, and so future flammability studies will require sufficient funding to do this.

While I demonstrated some key traits that are strongly correlated to shoot flammability and suggested that these can be used as surrogates for plant flammability, the challenge remains to use this relationship to determine the flammability of plants and vegetation in the field; further experimentation in field conditions are needed to confirm the finding. While several studies used leaf traits to understand landscape fire behaviour (Schwilk & Caprio 2011; Zylstra *et al.* 2016), a recent study by Tumino *et al.* (2019) has taken a step forward to link functional traits to flammability of vegetation in the field as measured from prescribed burning of species in damp and dry *Eucalyptus* forests of south-eastern Australia. They found that traits such as SLA and fuel bulk density were significantly associated with field-level flammability. Future studies should include the range of traits measured in this thesis (*Chapter 3*) to connect with the flammability of plants in either prescribed burn or controlled large-scale plant-level burning. Such knowledge is critical to bridge the gap between laboratory flammability studies and understanding field-scale fire behaviour using functional traits.

In *Chapter 4*, I demonstrated how the flammability of individual species affected the flammability of the fuel mixtures. It would be useful to examine the effect of proportional biomass of each constituent species on determining the flammability of the mixtures: i.e. how much biomass of a low flammability species is required before it starts to affect the flammability of a mixture? Also, future research should focus on the roles of functional traits in driving the mechanisms of mixed fuel burning.

5.6 Conclusion

This study demonstrates that shoot-level tests represent a better way of characterising plant flammability than leaf-level tests, and so helps bridge the gap between laboratory-based, small-scale flammability studies and whole-plant flammability. I recommend using shoot-level tests as a standard way of quantifying plant flammability, which could be used to answer a range of ecological and evolutionary questions in different biomes. Such work will produce a large dataset of species flammability globally, which can be used to map vegetation flammability and improve our predictions of fire behaviour, and how global change will affect fire regimes. Furthermore, this study demonstrated the strong relationship between functional traits and flammability at the shoot-level and identified key leaf traits, such as LDMC, leaf thickness and leaf lignin, and architectural traits, such as branching pattern, fuel fraction mass and fuel bulk density, that can be used as useful surrogates of plant flammability to predict flammability of species globally. Finally, this study demonstrates that flammability of fuel mixtures are different than those of the constituent species and are dominated by high flammability species. However, low flammability species in the mixtures make fires burn for a shorter duration with less heat released, demonstrating how they can be used in green firebreaks to help mitigate fire impacts. Overall, the findings from this thesis have provided new insights into plant flammability, its relationships with the functional traits and how it changes in mixed fuels. This has not only improved our understanding of how plants burn, it has also provided further insights on how vegetation can be managed to reduce the impacts of fire in an increasingly fire-prone world.

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